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Inheritance of resistance to loose smut in hybrids of Fulghum and Black Mesdag oats[1]

GEORGE M. REED

The present paper is concerned with the results obtained in an investigation of the inheritance of resistance to the Fulghum race of loose smut of oats in hybrids between Fulghum and Black Mesdag. The investigations of Reed (1927, 1929), and Reed and Stanton (1932) have demonstrated the existence of specialized races of both loose (*Ustilago Avenae* (Pers.) Jens.) and covered (*U. levis* (K. & S.) Magn.) smuts of oats which severely attack the Fulghum group of red oats. Several collections of these smuts have been obtained on Fulghum from various sources. Some other oat varieties, such as Canadian and Victor, have also proved to be susceptible. Fulghum, however, is very resistant to other highly specialized races of both oat smuts.

Black Mesdag has shown a high degree of resistance to all known races of loose smut, including the Fulghum race. No plants inoculated with the loose smut collected on Fulghum have been infected. It may be noted, however, that Black Mesdag has been found to be susceptible to a race of covered smut which is characterized by its ability to infect the Fulghum group of red oats (Reed 1932b).

Four crosses between Fulghum and Black Mesdag (Hybrids 29 to 32) were made in 1926, Fulghum being used as the female parent, and the first generation plants were grown in 1927. In 1928, inoculated F_2 plants were grown, some in the greenhouse and others in the field. Additional inoculated plants were grown in the field in 1929, and some uninoculated plants in 1931. Third, fourth, and fifth generation progenies were grown in various seasons from 1929 to 1934.

In all the experiments in which these hybrids were inoculated with loose smut, collection No. 13 was used. This collection was made by Mr. T. R. Stanton, Office of Cereal Crops and Diseases, Bureau of Plant Industry, Washington, D. C., on Fulghum oats at Lawton, Okla., in June 1925, and it was one of the original collections upon which the differentiation of the Fulghum race of loose smut was based.

The methods employed were those which have been used in all of my studies on the inheritance of smut resistance. The hulls were removed from the caryopses, which were then inoculated by dusting with the dry spores and germinated at a temperature of approximately 20°C. in sand

[1] Brooklyn Botanic Garden Contributions No. 70.

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with a low moisture content. Under these conditions, the seedlings usually emerged in four days and two to three days later were transplanted.

EXPERIMENTAL RESULTS WITH THE F_2 GENERATION

In table 1 are recorded the results obtained with the inoculated second generation plants of the four hybrids and also the two parental varieties. The data for the latter include all the results secured during 1928 to 1934, when they were grown along with the F_2 and later hybrid generations.

TABLE 1

Data obtained with the F_2 generation of hybrids 29–32—Fulghum×Black Mesdag, inoculated with Ustilago Avenae—Fulghum.

HYBRID NO.	NO. PLANTS	NO. INFECTED	PER CENT INFECTED
29	133	21	15.7
30	132	24	18.1
31	128	27	21.0
32	107	18	16.8
	500	90	18.0
		Reaction of parental varieties	
Fulghum	246	181	73.5
Black Mesdag	224	0	0

From the table, it will be noted that Fulghum gave 73.5 per cent infection, 181 plants out of a total of 246 being infected. In very few experiments were all of the Fulghum plants smutted. In contrast to Fulghum, Black Mesdag gave completely negative results; altogether, 224 plants were grown and none was infected.

In 1928 and 1929, 500 second generation plants belonging to the four hybrids were inoculated, and 90 (18 per cent) were infected. The percentage of infection in the four hybrids varied from 15.7 in Hybrid 29, to 21 per cent in Hybrid 31. The results indicate that resistance to smut is dominant and that segregation in the F_2 generation may occur on the basis of a three to one ratio.

EXPERIMENTAL RESULTS WITH THE F_3 GENERATION

There were two distinct groups of F_3 progenies available for study: (1) A group descended from F_2 plants which had been inoculated and survived, and (2) a group descended from F_2 plants which had not been inoculated. Results obtained with both groups of F_3 progenies are summarized in the distribution table 2. In this table the progenies are separated into classes,

based upon the percentage of infection. The number of progenies in each class, together with the total number of plants, the number infected, and the per cent infected, are shown. The reactions of the two groups of F_3 progenies are represented in the accompanying figure

TABLE 2

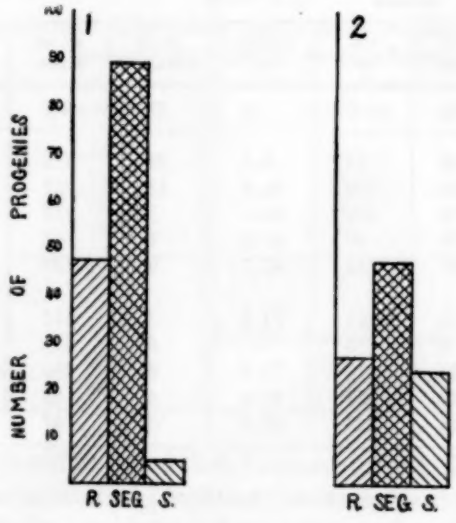
Data obtained with the F_3 generation of hybrids 29–32—Fulghum×Black Mesdag, inoculated with Ustilago Avenae—Fulghum.

CLASS CENTER	F_3 PLANTS INOCULATED WITH USTILAGO AVENAE—FULGHUM				F_3 PLANTS UNINOCULATED			
	NO. OF PROGENIES	NO. OF PLANTS	NO. INF.	PER CENT INF.	NO. OF PROGENIES	NO. OF PLANTS	NO. INF.	PER CENT INF.
0	47	1363	0	0	27	587	0	0
5	17	516	33	6.3	20	436	29	6.6
15	49	1293	190	14.6	12	257	38	14.7
25	17	495	123	24.8	5	110	27	24.5
35	3	78	30	38.4	4	92	29	31.5
45	3	67	32	47.7	6	139	65	46.7
55	2	62	34	54.8	5	114	63	55.2
65	0	0	0	0	6	128	83	64.8
75	1	24	18	75.0	6	130	99	76.1
85	1	20	17	85.0	4	97	83	85.5
95	1	24	23	95.8	3	67	62	92.5

On the basis of their reaction, the third generation progenies may also be classified as (1) resistant, in which no infected plants are found, (2) segregating, progenies in which the percentage of infected individuals is less than 50 per cent, and (3) susceptible, progenies which contain more than 50 per cent of smutted plants. The separation of the segregating and susceptible progenies is more or less arbitrary. It is possible that a segregating family consisting of 25 plants or less may contain more than 50 per cent of smutted individuals. A susceptible progeny also may show less than half of the plants infected. In general, however, the families may be distinguished on the basis indicated.

1. *F_3 progenies descended from inoculated F_2 plants.* As recorded in table 1, there were 500 F_2 plants inoculated, and 410 of these survived. Descendants of 141 of these plants were grown in the F_3 generation, the data being recorded in table 2. Of these, 47 progenies, containing 1363 plants, gave no infection, and are classified as resistant. There were 89 progenies classified as segregating, since they all contained some smutted plants, but the percentage of infection was less than 50 per cent. The 5

remaining progenies were classified as susceptible; 2 of these, however, were in the group whose class center is 55 per cent. Hybrid 31–F_3–93 grown in the field in 1929, contained 22 plants, of which 13 (59 per cent) were infected, and Hybrid 32–F_3–55 grown in the greenhouse in 1929, contained 40 plants of which 21 (52.5 per cent) were infected. These 40 plants were grown in two separate pots, and in one pot 10 plants were infected and in the other 11. The other 3 susceptible families gave 75, 85, and 95.8 per cent infection.



Reaction of F_3 progenies of Hybrids 29 to 32—Fulghum×Black Mesdag—to *Ustilago Avenae*—Fulghum.

1. F_2 plants inoculated 2. F_2 plants not inoculated

R.—Resistant progenies—No plants infected

Seg.—Segregating progenies—Percentage of infection 50 per cent or less

S.—Susceptible progenies—More than 50 per cent of the plants infected

As already noted, the F_2 data indicate that segregation takes place on the basis of a ratio of three resistant to one susceptible. The percentage of susceptible F_2 plants was somewhat low—actually, one F_2 plant out of five was smutted. The result of inoculating the F_2 plants is the elimination of all or practically all of the susceptible individuals; hence they would not be available for growing F_3 progenies. Consequently, in this particular group of F_3 progenies, descended from inoculated plants, we might expect one resistant progeny to two segregating. The results obtained are fairly close to expectation, since 47 progenies were resistant and 89 segregating.

The 5 susceptible progenies recorded may be due to the fact that susceptible F_2 individuals escaped infection and thus survived for growing the following generation. There may be some question as to whether the two progenies giving between 50 and 60 per cent infected plants were susceptible or segregating. There can, however, be no reasonable doubt about the other three, which gave 75 per cent or more infection.

2. *F_3 progenies descended from uninoculated F_2 plants.* As recorded in table 2, there were 98 F_3 progenies grown from uninoculated F_2 plants. These were classified as 27 resistant, 47 segregating, and 24 susceptible. The 27 resistant progenies contained 587 plants. Of the 47 segregating progenies, 20 are found in the group whose class center is 5, 12 additional ones are found in the group whose class center is 15, and the remaining ones are distributed somewhat uniformly in the three groups with class centers of 25, 35, and 45.

The susceptible families are distributed in all the groups with class centers from 55 to 95. None of the progenies gave 100 per cent infection, but it may be noted again that the susceptible Fulghum parent rarely ever contained 100 per cent infected plants in a given experiment.

Since the F_2 plants had not been inoculated, the susceptible individuals were not eliminated; consequently, F_3 progenies might be grown from such susceptible plants. Further, if segregation in the F_2 generation takes place on the basis of a ratio of three to one, we would expect, among the F_3 progenies descended from uninoculated F_2 plants, 1 resistant, 2 segregating, and 1 susceptible. The results obtained harmonize fairly well with expectations.

EXPERIMENTAL RESULTS WITH THE F_4 GENERATION

A series of 256 F_4 progenies was grown in the course of the experiments. All of these had descended from uninoculated second generation plants. Most of them also had descended from uninoculated individuals of F_3 progenies. The reaction of the third generation, however, was known by the behavior of inoculated sister plants. The F_4 progenies were descended from three distinct types of F_3 families—resistant, susceptible, and segregating.

1. *F_4 families descended from resistant F_3 progenies.* There were 15 resistant F_3 progenies, represented by 3 to 11 F_4 families, a total of 108 being grown. These contained 1726 plants. Only 6 smutted plants, distributed among 5 different families, were observed. Thus the resistance manifested in the third generation is evident in the F_4 descendants.

2. *F_4 families descended from susceptible F_3 progenies.* There were 72 F_4 families grown from 16 F_3 progenies classified as susceptible, the percent-

ages of infection ranging from 54.1 to 95.4 per cent. All of the 72 F_4 families contained some smutted plants, although the amount of infection varied greatly, most of them giving more than 50 per cent infection. The lowest percentage was 7.1, while in two families all the plants were smutted.

Since the F_3 progenies were classified as susceptible, we might expect that all of the F_4 families would also be susceptible. However, many families contained entirely too few infected plants to be classified as susceptible. It is interesting to note the details for the F_3 progenies from which 5 or more F_4 families were grown.

F_3 generation—per cent inf.		*F_4 generation—per cent inf.*	
Hybrid 29–F_3–204	84.0	7 families	47.3– 78.9
" 29–F_3–210	80.0	5 "	58.8– 85.0
" 30–F_3–208	91.6	5 "	57.8– 89.4
" 31–F_3–207	90.4	5 "	10.5– 55.5
" 32–F_3–201	95.4	5 "	17.6–100.0
" 30–F_3–201	54.1	10 "	25.0– 75.0
" 31–F_3–210	70.0	5 "	50.0–100.0
" 32–F_3–205	68.1	10 "	7.1– 90.0

The first five F_3 progenies gave 80 to 95.4 per cent infection; among the F_4 families, however, the percentages ranged from 10.5 to 100 per cent. The last three F_3 progenies gave 54.1 to 70 per cent, and the range of infection in the F_4 generation varied from 7.1 to 100 per cent.

3. *F_4 families descended from segregating F_3 progenies.* There were 8 F_3 segregating progenies, represented by 76 F_4 families, the data for which may be summarized as follows:

F_3 generation—per cent inf.		*F_4 generation—range of infection*		
Hybrid 29–F_3–203	12.5	8 families		All resistant
" 29–F_3–205	8.3	8 "	resistant; 2 gave	5.0–10.5
" 30–F_3–202	4.0	6 "	" 4 "	6.2–12.5
" 30–F_3–204	5.0	10 "		All resistant
" 31–F_3–201	12.5	4 "	resistant; 6 gave	5.2–90.9
" 31–F_3–204	6.2	2 "	" 8 "	10.0–80.0
" 31–F_3–208	33.3	5 "	" 5 "	5.5–15.0
" 32–F_3–211	5.0	7 "	" 1 "	10.0

The results are not sufficiently extensive to furnish the basis for any definite conclusions. The behavior of some of the individual families, however, is particularly interesting. Hybrid 29–F_3–203 and Hybrid 30–F_3–204 contained some smutted plants, but all the F_4 families were completely resistant. Hybrid 32–F_3–211 contained 1 smutted plant, while in the F_4 generation only 2 infected individuals in one of the 8 progenies were ob-

served. From the remaining 5 F_3 progenies giving 4 to 33.3 per cent infection, 50 F_4 families were grown, and half of these were resistant and half contained smutted plants, the percentage varying from 5 to 90.9 per cent. On the basis of the general behavior of the F_2 and F_3 generations, we might expect the three groups of F_4 families—resistant, segregating, and susceptible. It is obvious, however, that a very large proportion of the F_4 families belong to the resistant group.

EXPERIMENTAL RESULTS WITH THE F_5 GENERATION

A few F_5 families, descended from 10 resistant F_3 progenies, were grown, the latter being derived from uninoculated F_2 plants. In the F_4 generation the families were also resistant, although in three cases sister progenies contained a smutted plant. Altogether, there were 24 F_5 generation families containing 447 plants, and none was infected. Thus the resistance observed in the F_3 and F_4 generations is continued through the fifth generation.

REACTION OF SOME F_3 PROGENIES TO USTILAGO LEVIS—FULGHUM

We have already mentioned the fact that both Fulghum and Black Mesdag, the parental varieties used in these crosses, are susceptible to a newly discovered race of covered smut (Reed, 1932b). No attempt to use this race in an extensive series of experiments with these hybrids has been made. However, in 1932, 24 F_3 progenies of Hybrid 31, inoculated with it, were grown. All of them contained smutted plants, the range of infection varying from 4.5 to 85.7 per cent. Neither of the parents, Fulghum or Black Mesdag, has given, as a rule, very high percentages of infection, although Fulghum has appeared to be somewhat more susceptible than Black Mesdag.

DISCUSSION AND SUMMARY

In recent years several investigators have published data on the inheritance of smut resistance in oat hybrids, and most of the literature up to 1932 has been reviewed in one of my papers (Reed, 1932a). Since then, some additional publications have appeared, including Coffman et al. (1931), Johnson (1933), Nicolaisen (1934), Schattenberg (1934), Stanton, Coffman and Tapke (1934), and Stanton, Reed and Coffman (1934). Many different oat varieties have been used in the crosses involved in the studies carried out by these investigators.

The variety Fulghum was used as one parent in some studies by Reed and Stanton (1925). Fulghum was crossed with Swedish Select, and a series of 92 F_3 progenies inoculated with *Ustilago Avenae* was grown. Fulghum

was resistant to this particular collection of loose smut, while Swedish Select was moderately susceptible. Of the 92 families grown, 25 gave no infection, 55 gave less than 40 per cent infection, and 12 were classified as susceptible. While the data were not extensive enough to determine definitely the mode of inheritance of the resistant quality, they indicated that resistance was dominant and that segregation probably occurred on the basis of a three to one ratio.

Black Mesdag has frequently been employed in hybridization experiments involving the study of the inheritance of smut resistance. It is very valuable for this purpose on account of its very great resistance to most known races of both loose and covered smut. I have used this variety in crosses with Hull-less, Silvermine, and Early Champion (Reed, 1927, 1928, 1934). Results with the F_2 generation indicated that resistance was dominant and that segregation occurred on the basis of three resistant plants to one susceptible. Data for the F_3 and later generations harmonized fairly well with this interpretation. The results were secured with definite specialized races of both loose and covered smut to which Black Mesdag was completely resistant, and Hull-less, Silvermine, and Early Champion were susceptible.

It is interesting to note that the studies on the hybrids of Fulghum and Black Mesdag in which a very different specialized race of loose smut was employed, also indicate that resistance is dominant and that segregation occurs on the basis of a three to one ratio. The data for the F_2 and F_3 generations are in harmony.

The question may be raised as to why Fulghum rarely ever gave 100 per cent infection with the particular race of loose smut used in these experiments. Two other varieties, Frazier and Kanota, which have been developed as selections from Fulghum, have given somewhat similar results. Other selections of Fulghum, however, have given higher percentages of smutted plants. Further, the variety Canadian has been inoculated at different times with this same collection of loose smut, and frequently has given 100 per cent of smutted plants.

Another problem is involved in the occurrence of occasional smutted plants in the F_3 and F_4 generations. In a few cases, completely resistant F_3 progenies gave rise to F_4 families in which a smutted plant was observed. There were also at least two cases in which a small amount of smut was found in the F_3 generation, but all of the F_4 progenies grown were resistant.

As noted above, the very susceptible F_3 progenies gave rise to F_4 families showing great variation in the amount of smut, although it might have been expected that all would be susceptible. It is true that smutted plants were found in all of these F_4 families and that most of them contained

more than 50 per cent of smutted plants. Among all the progenies, however, the percentage of infection ranged from 7.1 to 100 per cent.

All of the 24 fifth generation families grown were descended from resistant F_3 and F_4 generations. The results indicate that resistant selections through a series of generations may easily be secured. No detailed study of the inheritance of smut resistance in comparison with the inheritance of the morphological characters of the parental varieties has been made. However, the few resistant F_5 families grown combine in various ways the characters of Fulghum and Black Mesdag, especially as to color of glumes, presence or absence of awns, size and shape of the caryopsis. Some of the families are almost identical with Fulghum in morphological appearance.

Finally, it may be emphasized that the reaction of these hybrids to a specific race of loose smut has been determined. Quite different results would have been obtained if other races had been used, such as the Missouri races of loose and covered smut, to which both varieties are resistant, or the Fulghum race of covered smut, to which both are susceptible.

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The anatomy of the stem in the Lejeuneae[1]

ALEXANDER W. EVANS
(WITH EIGHT FIGURES)

INTRODUCTION

The Lejeuneae represent one of the largest and most natural groups of the Hepaticae and constitute the predominant part of the hepatic vegetation in many tropical regions. Following the example of Spruce (1885, p. 74) most writers divide them into two subgroups: the Holostipae, characterized by undivided underleaves; and the Schizostipae, characterized by bifid underleaves. In 1908 Lacouture (p. 102) separated from the Schizostipae, as a third subgroup, the "Lejeunea paradoxaux," most of the members of which are characterized by the duplication of the underleaves or by their absence. This subgroup, which may be designated the "Paradoxae," includes some of the most highly specialized and reduced of the Lejeuneae. Each of the three subgroups is further divided into a number of more or less clearly defined genera, the distinctive characters of which have been derived from the peculiarities of the leaves, underleaves, and floral organs, as well as from the general morphology of the plants.

The anatomy of the axial organs, however, has received but little attention from students of the Hepaticae. It has apparently been assumed that these organs were simple and uniform in structure and that they were therefore of slight interest to either the morphologist or the taxonomist. Such is not the case. Although the stems never attain the high degree of complexity found in the Polytrichaceae and certain other families of the Bryales (see, for example, Haberlandt, 1886, p. 392), they exhibit throughout the group a distinct differentiation into a unistratose cortex and a medulla, and these structures present a wide range of diversity in passing from the more robust genera of the Holostipae to the more delicate genera of the Schizostipae and Paradoxae. From the standpoint of the taxonomist the histological features of the stems and branches yield important characters, which supplement in many cases the characters derived from the leaves and underleaves. The histological characters, in fact, are fully as significant in the Lejeuneae as in certain other groups of the Hepaticae, in which their value is becoming more and more widely recognized. In the following account the more complex types of stem-structure will be considered first, and it is perhaps safe to assume that such types are relatively primitive and that they have given rise to the less complex types by processes of simplification and reduction.

[1] Contribution from the Osborn Botanical Laboratory.

THE ANATOMY OF THE STEM IN SELECTED SPECIES

Holostipae

BRYOPTERIS FILICINA (Swartz) Nees. According to published records *B. filicina* has a wide distribution in tropical America. The plants usually grow on the trunks of trees and show a differentiation into a prostrate caudex and spreading secondary stems. The latter are stiff and firm and maintain their rigidity whether wet or dry. They attain a length of 10–15 cm. and give off widely spreading branches at short intervals. Since the branches are normally limited in growth they give rise to distinctly pinnate branch-systems, which spread in approximately horizontal planes. The

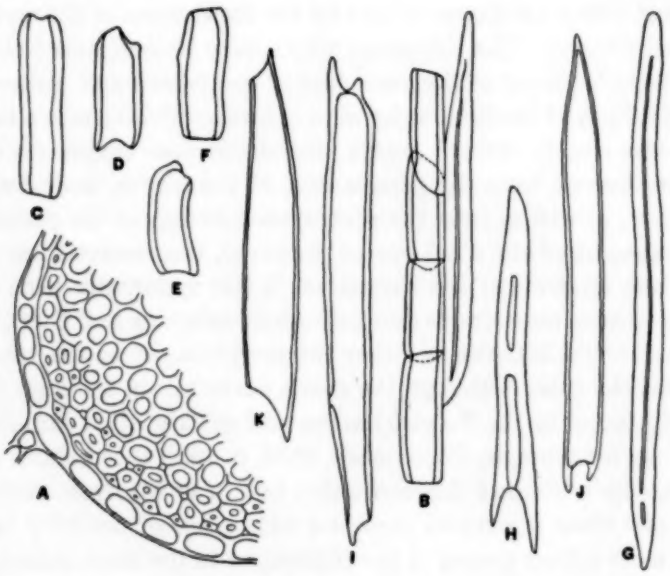


Fig. 1. *Bryopteris filicina* (Swartz) Nees. A. Cross-section of secondary stem, underleaf attached at left. B. Four cortical cells and an adjoining medullary cell. C–F. Cortical cells. G–J. Medullary cells. All, ×225.

axial organs are more or less deeply pigmented, and the stem (or main axis) may attain a width of 0.4 mm. The example illustrated by a cross-section (fig. 1, A) had a width of 0.3 mm. and a thickness of 0.25 mm., thus showing a slight dorsiventral compression. In such cross-sections the pigmentation is clearly evident, and the color varies from a pale yellow to a deep orange brown. Although all the walls are pigmented the deepest shades are found in the peripheral layers of the medulla, and the dorsal layers are

more deeply pigmented than the ventral. Toward the interior of the medulla the color rapidly becomes paler, and the walls of the cortical cells are likewise paler than those of the peripheral medullary cells.

The number of cortical cells in a cross-section varies from thirty to thirty-five, indicating approximately the number of longitudinal rows in which the cells are arranged. The cells, which appear more or less flattened, have a width of 15–25μ and a thickness of 10–12μ. The outer tangential walls are, in some cases at least, distinctly thinner than the inner tangential and radial walls, but even these rarely exceed 4μ in thickness.

The medulla is sixteen to twenty cells thick in its shorter diameter. The cells of two or three peripheral layers have strongly thickened walls and small lumina. These cells are 10–14μ in diameter, and the thickness of the wall between two lumina may be as much as 8μ. The cells in the interior have thin walls and large lumina. Their diameter, in many cases, is as much as 20μ, but their walls may be only 1–2μ thick, except for more or less distinct triangular thickenings at the angles. The transition between the peripheral and interior cells is gradual. In the walls of the peripheral layers the middle lamellae stand out clearly, not only in the walls between medullary cells, but also in the walls between medullary and cortical cells. Toward the interior the middle lamellae become less and less distinct and are soon no longer discernible. Pits can be demonstrated here and there in a cross-section but are not conspicuous.

The study of cross-sections gives only an inadequate idea of the cortical and medullary cells and of the differences between them. To show the true forms of the cells longitudinal sections are helpful, but macerated preparations are even more satisfactory. These can be easily obtained by treating fragments of stems with Schulze's maceration mixture. If the fragments are heated for a few seconds in the mixture and then washed thoroughly with water they can readily be torn apart under a dissecting microscope. In such preparations the cortical cells can be distinguished from the medullary cells by their relatively short length. This is, in most cases, between 25μ and 70μ, whereas the length of the medullary cells is between 120μ and 220μ. Speaking generally, therefore, the medullary cells are three or four times as long as the cortical cells. Figure 1, B, which represents four cortical cells in optical radial section, together with an adjoining medullary cell, brings out this relationship clearly. In figure 1, C–F, four cortical cells in surface-view are shown. It will be seen from these figures that the cortical cells are approximately rectangular in longitudinal section, with parallel sides. The longitudinal walls, whether tangential or radial, are uniformly thickened, but the end walls are thin throughout the greater part of their extent, thus allowing communication between the

cells in a longitudinal direction. The ends of the cells, in many cases, slightly overlap or develop one or two short and blunt projections.

The majority of the cells at and near the periphery of the medulla, as shown in figure 1, B, G, are in the form of short sclerenchyma fibers, tapering at each end to a sharp or blunt point. The lumina of these cells are reduced to narrow canals and may be entirely obliterated at the ends. Even in other parts of the cell, as shown in figure 1, G, the lumen may be bridged across by deposits of cell-wall substance. Deviations from the ideal fiber-like form are not infrequent. In the example shown in figure 1, H, one end is pointed and without a lumen, but the other end is broad and runs out into two slender pointed processes with an area of thin cell-wall between them. This cell, too, shows a bridge of cell-wall substance at about the middle. The cell illustrated in figure 1, I, which was situated at some little distance from the periphery, shows an area of thin cell-wall at each end. At the upper end the thick longitudinal wall extends as two short solid processes, but at the lower end the wall gradually thins out. In this cell a pit is represented in optical section on the left-hand side. Cells from the interior of the medulla, two examples of which are shown (fig. 1, J, K), are similar in form to the cell just described but have thinner walls. The cell represented in figure 1, J is pointed at one end and bears two solid projections at the other, with a thin, almost transverse area between them; but the cell represented in figure 1, K, shows a thin oblique area at each end, with a single solid point projecting beyond it. It is evident, from the examples figured, that the various types of medullary cells intergrade into one another, however different the peripheral cells may be from the interior cells. Except in the extreme fiber-like types the cells show more or less effective arrangements for the passage of liquids in a longitudinal direction. The scarcity of pits in the longitudinal walls, however, would apparently make the passage of liquids in transverse and oblique directions far more difficult. In all probability pits are more abundant in young medullary cells and become more or less filled up as the cells reach maturity.

The structure of the stem in *Bryopteris filicina* does not correspond very closely with either of the types distinguished by Herzog (1925, p. 67). It agrees with his second type, as exemplified by *Cephalozia connivens* (Dicks.) Lindb., in having a unistratose cortex, but the cortical cells differ in being relatively smaller and in having somewhat thicker walls. The medulla, moreover, is more highly differentiated than that of the *Cephalozia*, since it shows an external layer of thick-walled cells enclosing an internal core of cells with thinner walls. If the cortex were absent the stem, in cross-section at least, would resemble Herzog's first type, as exemplified by *Plagiochila asplenioides* (L.) Dumort., in which a pluristratose cor-

tex of thick-walled cells surrounds a medulla composed of thin-walled cells.

PTYCHANTHUS STRIATUS (Lehm. & Lindenb.) Nees. This widely distributed species of tropical Asia and Africa is found on both rocks and trees. It resembles *Bryopteris filicina* in being differentiated into a prostrate caudex and widely spreading secondary stems. The latter attain a length of 8–10 cm. and give rise to numerous branches, most of which are

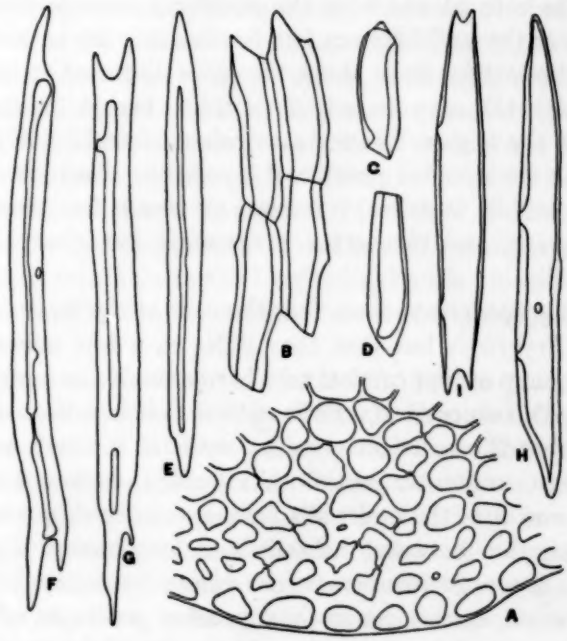


Fig. 2. *Ptychanthus striatus* (Lehm. & Lindenb.) Nees. A. Cross-section of secondary stem, ventral portion. B. Group of four cortical cells, surface-view. C, D. Cortical cells, radial view. E–I. Medullary cells. All, ×225.

sooner or later limited in their growth. In this way, much as in the *Bryopteris*, flat pinnate branch-systems are developed, the axial organs of which are firm and rigid whether wet or dry. The stem studied by the writer was about 0.45 mm. in width and 0.3–0.35 mm. in thickness. Cross-sections show a deep yellow color in the outer part, fading rather abruptly to a pale yellow or cream color in the interior.

The number of cortical cells in a cross-section (fig. 2, A) is approximately fifty, and these cells are very similar in appearance to the peripheral medullary cells, except that their external walls are thinner and

their cavities larger. The cortical cells have a rectangular outline and are 20–30μ in width by 12–16μ in thickness. The external walls are only 3–4μ thick and thus stand in rather sharp contrast to the radial walls, which are about 8μ thick.

The medulla is about sixteen cells across from top to bottom and is bounded on the outside by two or three layers of very thick-walled cells. The interior is composed of cells with much thinner walls, and the transition from the external layers to the interior is less gradual than in the *Bryopteris*. The cells at and near the periphery average about 18μ, and the thickness of the wall between two lumina may be as much as 8–10μ. The cells in the interior have about the same diameter as the peripheral cells, but their walls may be only 2–3μ thick, except for the triangular thickenings at the angles. Pits are everywhere abundant in the medulla, not only in the thick-walled peripheral layers, but also in the thin-walled interior. The middle lamellae, however, are much less distinct than in *Bryopteris filicina*, and the cortex is therefore less clearly marked off from the medulla.

Macerated preparations show that the cells of the stem are much like those of the *Bryopteris* but that they differ in a few minor details. In figure 2, B, a group of four cortical cells is represented in surface-view and in figure 2, C, D, two cortical cells in optical radial section. These figures show clearly that the radial longitudinal walls of the cells are uniformly thickened, that the outer tangential walls are thinner than those adjoining the medulla, and that the end-walls have extensive thin areas, allowing easy communication between the cells in a longitudinal direction. The ends of the cells are, in some cases, cut across transversely or obliquely but, in other cases, extend out as short pointed processes, which may be thin-walled throughout or show a deposit of cell-wall substance at the tip. These features show that the cortical cells, as in the *Bryopteris*, may overlap at their ends or be otherwise more or less firmly wedged together. Their length usually varies between 40μ and 70μ, but an occasional cell may be as much as 120μ long.

The medullary cells are mostly 150–250μ long. Those at the periphery, like the example represented in figure 2, E, are, in many cases, in the form of short sclerenchyma fibers with pointed ends. Such cells are essentially like the peripheral fibers found in the *Bryopteris*, except that their lumina tend to be a little broader. Two other cells from the peripheral region, in which the ends have developed irregular solid projections of cell-wall substance, are shown in figure 2, F, G. In figure 2, F, each end exhibits a thin area in connection with the projections, but in figure 2, G, both ends

are solid. In figure 2, F, the lumen of the cell is strongly contracted below the middle, and the wall on the right-hand side shows two partially obliterated pits. In the upper pit a deposit of cell-wall substance stretches across the opening of the canal, leaving a small cavity next to the pit-membrane; in the lower pit the deposit fills the bottom of the canal only. Figure 2, H, represents a medullary cell just inside the peripheral sheath. In this cell both ends are pointed, and the lower end is thick-walled throughout. On the left-hand side the thick cell-wall extends almost to the upper end but, on the right-hand side, thins out at about the middle. The upper end of the cell and the upper half of the right-hand side are relatively thin-walled. Three pits are visible in this cell, two in profile-view on the left-hand side and one in surface-view a short distance below the middle. In figure 2, I, a cell from the interior of the medulla is represented. The longitudinal walls of this cell are about as thick as the wall at the upper end of the cell shown in figure 2, H; each of the thin-walled ends has developed two pointed processes; and two well-marked pits are visible on the left-hand side. Pits in the longitudinal walls are apparently much more abundant in *Ptychanthus striatus* than in *Bryopteris filicina*.

STICTOLEJEUNEA KUNZEANA (Gottsche) Schiffn. In this Andean species another plant is met with in which the shoot is differentiated into a prostrate caudex and flat pinnate branch-systems. These are unusually robust and may attain a length of 20 cm. or even more. In the plant selected for study the main axis had a width of 0.35–0.4 mm. and a thickness of 0.3–0.33 mm. Although the walls of the leaf-cells are colorless or nearly so, the walls of the axial organs are distinctly pigmented with varying shades of yellow or brown. In cross-sections all the walls appear pigmented, but a deep orange–brown peripheral band stands in sharp contrast to the pale yellow or cream-colored interior. This band is four or five cells wide at top and bottom and two or three cells wide on the sides.

The morphological differences between the cortical cells and the peripheral medullary cells appear very slight in cross-section (fig. 3, A). They are both characterized by very thick walls and small cavities, and the boundaries of the cells are clearly indicated by the more deeply pigmented middle lamellae. In many of the cells the cavities are in the form of narrow slits, lying parallel with the edge of the section. The cortical cells, which number sixty to seventy in cross-sections, are mostly 12–16μ in width by 10–12μ in thickness, and the external walls often attain a thickness of 6–8μ.

The medulla is sixteen to eighteen cells thick from top to bottom. The

cells of the peripheral portion are mostly 15–20μ in diameter but may be as much as 25μ, and the wall between two cavities may be as much as 10μ thick. These cells therefore, in their transverse dimensions rival or even slightly exceed the cortical cells. The internal cells of the medulla average

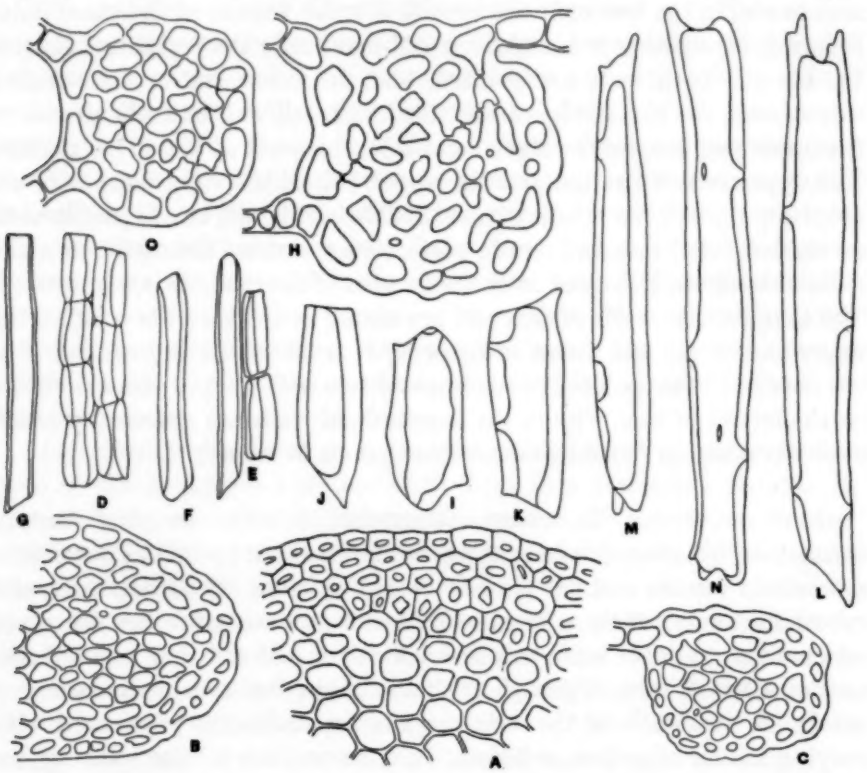


Fig. 3. A. *Stictolejeunea Kunzeana* (Gottsche) Schiffn. Cross-section of secondary stem, dorsal portion. B. *S. squamata* (Willd.) Schiffn. Cross-section of stem, lateral half. C–G. *Neurolejeunea Breutelii* (Gottsche) Evans. C. Cross-section of stem, lobe attached at left. D. Group of cortical cells, surface-view. E. Two cortical cells and an adjoining medullary cell, radial view. F, G. Medullary cells. H–N. *Omphalanthus filiformis* (Swartz) Nees. H. Cross-section of stem, lobe and lobule of leaf attached at left, lobe of another leaf at right. I–K. Cortical cells. E–N. Medullary cells. O. *Leucolejeuna xanthocarpa* (Lehm. & Lindenb.) Evans. Cross-section of stem, leaf attached at left. All, ×225.

about 20μ in diameter, but an occasional cell may be as much as 30μ across. The walls are only 2–3μ thick, except for the indistinct triangular thickenings at the angles. Pits are present in all parts of the medulla but are not always easy to demonstrate; in the peripheral layers they seem to be more frequent in the radial than in the tangential walls.

The axial cells of *Stictolejeunea Kunzeana* in macerated preparations are much like those of *Bryopteris filicina* and *Ptychanthus striatus*. The distinctions between the cortical cells and the peripheral medullary cells, however, are less pronounced. The cortical cells, for example, although only 30μ long in some cases, are usually 60–80μ long and may attain a length of 100μ. Since the length of the medullary cells is mostly between 140μ and 240μ, the shortest medullary cells are not much longer than the longest cortical cells.

STICTOLEJEUNEA SQUAMATA (Willd.) Schiffn. The second species of *Stictolejeunea* to be considered is widely distributed in tropical America and grows on both trees and rocks. Although the plants form irregularly pinnate branch-systems, comparable with those of *S. Kunzeana*, there is no differentiation into a prostrate caudex and spreading secondary stems. The branch-systems, on the contrary, are produced by the branching of the prostrate primary stems and are themselves prostrate or very slightly ascending. The plants are therefore less exposed to the dangers of mechanical injury and desiccation than are those of *S. Kunzeana*. The stems of *S. squamata* are about 0.2 mm. in width by 0.15 mm. in thickness. The pigmentation of the stem, as seen in cross-sections, is less pronounced than in *S. Kunzeana*, the contrast in color between the orange yellow peripheral layer and the paler yellow interior is less marked, and the change from one to the other is more gradual. A cross-section (fig. 3, B) brings out scarcely any morphological differences between the cortical cells and the peripheral medullary cells: both are characterized by uniformly thickened walls and more or less reduced lumina. The cortical cells, of which thirty-five to forty are visible, measure 10–20μ in width by 8–15μ in thickness, and the cells on the dorsal surface are distinctly larger than those on the ventral surface. The external walls are mostly 4–6μ thick.

The medulla is only eight or nine cells thick in its shorter diameter, and the peripheral cells with uniformly thickened walls occupy only one or two layers. The next layers are transitional in character, and the internal cells are distinguished from the peripheral cells by their much thinner walls, with more or less distinct triangular thickenings at the angles. The medullary cells average about 15μ in diameter, but the largest are 20μ wide. Some of the medullary cells, therefore, are larger in their transverse dimensions than some of the cortical cells.

NEUROLEJEUNEA BREUTELII (Gottsche) Evans. The species of *Neurolejeunea* are smaller and less definite in habit than any of the forms so far discussed. In the species under consideration the plants have a deep olive

green or olive brown color and grow in loose tufts on rocks and trees. The individual stems are mostly 3–5 cm. in length and give off branches sparingly and irregularly. In the plant examined the stem had a width of about 0.15 mm. and a thickness of about 0.12 mm., but more slender stems are not infrequent. A brown pigmentation of all the cell-walls is shown in cross-sections, and the difference in shade between the darker peripheral portion and the paler interior portion is very slight. The morphological differences between the cortex and medulla, as brought out by cross-sections (fig. 3, C), are by no means striking. The cortical cells, which number about eighteen, measure 10–20μ in width by 10–15μ in thickness, and their external walls are about 4μ thick.

The medulla, in most cases, is only five cells across from top to bottom. The cells composing it average about 12μ in diameter, although an occasional cell may be as much as 20μ in width. The walls are mostly only 2–3μ thick but show indistinct triangular thickenings at their angles. Since the walls of the peripheral cells are only a little thicker than those of the interior cells, the medulla is not differentiated into a thick-walled sheath surrounding a thin-walled core. Pits and middle lamellae are difficult to demonstrate.

Individual cells or groups of cells obtained by maceration are represented in figure 3, D–G, and indicate that the cell-differentiation is relatively slight. Figure 3, D, shows a group of cortical cells which are still in contact. The thick longitudinal radial walls appear in optical section, and the transverse or slightly oblique end-walls have extensive thin areas. In figure 3, E, two cortical cells in optical radial section and an adjoining medullary cell are shown in their relative positions. The cortical cells bring out the fact that the outer wall is thicker than the inner, and the lower cell shows a short pointed projection of cell-wall substance. The medullary cells, represented in figure 3, F, G, are several times as long as broad and are characterized by their more or less thickened longitudinal walls and thin end-walls. The latter, which may be transverse or oblique, run out, in some cases, into short, bluntly pointed processes. Apparently none of the cells have the form of sclerenchyma fibers. The cortical cells are mostly 25–50μ in length and the medullary cells, 90–120μ.

OMPHALANTHUS FILIFORMIS (Swartz) Nees. Few species are more abundant in the lower mountains of the American tropics than *O. filiformis*. The plants form loose, yellowish green tufts on various substrata and assume, in most cases, an ascending or suberect position. The main stems are 5–10 cm. in length and give off branches sparingly and irregularly. Cross-sections (fig. 3, H), which are approximately circular,

have a diameter of about 0.15 mm. and show a uniform orange-yellow pigmentation throughout. At first sight the sections seem to be undifferentiated into cortex and medulla, since all the cells have uniformly thickened walls. Closer inspection, however, shows that the transverse dimensions of the cortical cells are a little larger than those of the medullary cells, and the study of macerated tissues brings out other and more important distinctions. The cortical cells, which number twelve to fifteen in a cross-section, bulge outward and give the periphery a crenulate appearance. They are mostly 20–30μ in width by 20–25μ in thickness, and the external walls, in many cases, are 8–12μ thick. In some of the radial walls pits can be demonstrated, as shown in the lower part of figure 3, H.

The medulla is mostly six or seven cells across, and there is no distinction between the peripheral and internal portions. The cells average about 16μ in diameter, and their walls are usually 8–12μ thick. Although the middle lamellae are scarcely distinguishable, pits are conspicuous and can be demonstrated, not only in the walls between medullary cells, but also in the walls between medullary and cortical cells. Ample provision, therefore, is apparently present for communication between cells in transverse directions.

The medullary cells, in macerated preparations, are seen to be three or four times as long as the cortical cells. The latter are mostly 50–80μ in length but may be as much as 100μ. Figure 3, I, represents a cortical cell in surface-view; figure 3, J, K, two cortical cells in optical radial section. The radial walls of the cell shown in figure 3, I, are strongly thickened and show no pits, but the upper end-wall shows two thin areas and the lower end-wall one. In all probability the upper end of the cell abutted against two cells belonging to different rows, and the thin areas afforded communication with those cells. Similar relationships, in some cases, can be demonstrated between cells on intact stems. The short pointed projections of cell-wall substance at the ends of the cell doubtless served to increase the firmness of the union with adjoining cells. In the cells shown in figure 3, J, K, the walls on the right-hand side represent the outer tangential walls. In figure 3, J, this wall is distinctly thicker than the inner tangential wall, which is apparently destitute of pits; in figure 3, K, on the contrary, the two tangential walls are subequal in thickness and the inner wall shows two pits. The oblique end of the cell shown in figure 3, J, and the two oblique ends of the cell shown in figure 3, K, indicate more or less overlapping.

The medullary cells are apparently never developed in the form of sclerenchyma fibers with pointed ends. The characteristic examples repre-

sented in figure 3, L–N, show that the ends are broad, although they may be either transverse or oblique. All of the cells figured show at each end from one to three short processes of cell-wall substance, and the processes at the upper end of figure 3, L, have given off secondary processes. Except in the case of the upper end of the cell shown in figure 3, M, where the wall is uniformly thickened, each end shows one or two thin areas. The thick side-walls of the cells figured show a number of pits in profile-view, and figure 3, N, shows two pits in surface-view. These pits are in the form of narrow ellipses running longitudinally and are similar to the pits found in the bast-fibers of *Antitrichia curtipendula* (Hedw.) Brid., as figured by Haberlandt (1886, *pl. 21, f. 11*). The medullary cells of *Omphalanthus filiformis* are mostly 240–360μ in length and thus tend to be longer than in any of the preceding forms.

LEUCOLEJEUNEA XANTHOCARPA (Lehm. & Lindenb.) Evans. The pale glaucous green plants of *L. xanthocarpa* grow on the bark of trees and form thin depressed mats. The species has an unusually wide distribution and is found not only in the tropical and subtropical portions of North and South America but also in Africa and the East Indies. The prostrate stems, which are subterete, branch irregularly and are mostly 2–5 cm. in length by 0.1–0.15 mm. in diameter. Cross-sections (fig. 3, O) are, in general, much like those of *Omphalanthus filiformis*. The cell-walls, for example, although of a pale yellow color, are uniformly pigmented throughout, the cells are everywhere thick-walled; and the visible distinctions between the cortical and medullary cells are relatively slight. The cortical cells, which number about fifteen, are 15–25μ in tangential width by 15–20μ in radial width, and their external walls are 4–8μ thick. The periphery of a section scarcely appears crenulate, although some of the cells bulge slightly. The medulla is four or five cells across, the medullary cells average about 14μ in diameter, and the walls are 6–8μ thick. The thickenings, however, owing to the frequency of pits, present the appearance of being brought about by the coalescence of trigones. The pits can be demonstrated, as in the *Omphalanthus*, not only in the walls between medullary cells, but also in the walls between medullary and cortical cells and in the radial walls between cortical cells.

ARCHILEJEUNEA SPRUCEANA Steph. The species of *Archilejeunea* have the shoot differentiated into a prostrate primary stem and spreading secondary stems. The latter, which are relatively short, are either simple or sparingly and irregularly branched. The plants do not form, therefore, complicated pinnate branch-systems like those found in *Bryopteris*, *Ptychanthus*, and *Stictolejeunea Kunzeana*. The species here considered is

abundant in eastern South America and grows on the bark of trees. The plants are reddish green or brownish green, and the secondary stems have a length of 2.5–5 cm. and a diameter of about 0.15 mm. In spite of the difference in habit between *A. Spruceana* and *Leucolejeunea xanthocarpa*, the structure of the stem is much the same, although the contrast in size between the cortical and medullary cells is a little more pronounced in the *Archilejeunea*. Cross-sections show a pigmentation with pale brownish yellow throughout, with but slight variation in shade. The cortical cells

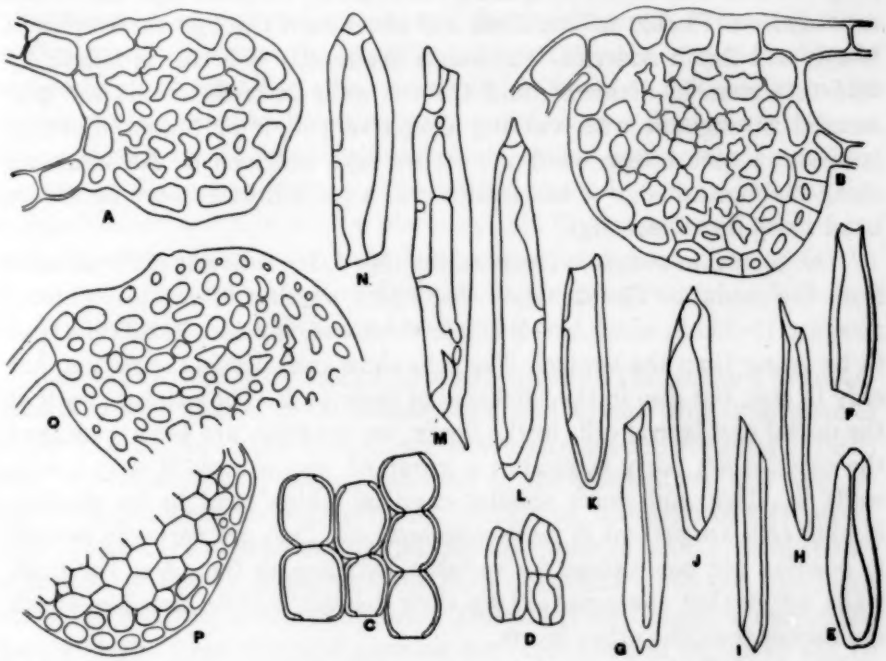


Fig. 4. A. *Archilejeunea Spruceana* Steph. Cross-section of stem, leaf attached at left. B–N. *Mastigolejeunea auriculata* (Wils. & Hook.) Schiffn. B. Cross-section of stem, lobe and lobule of leaf attached at right, lobe of another leaf at left. C, D. Groups of cortical cells. E–N. Medullary cells. O, P. *Thysananthus amazonicus* (Spruce) Schiffn. O. Cross-section of mature stem, lobe attached at left. P. Cross-section of young stem, ventral portion. All, ×225.

(fig. 4, A) number about fifteen and measure 20–25μ in width by 15–20μ in thickness. The external walls, in most cases, are 4–6μ thick but may be as much as 8μ thick. The medullary cells average about 13μ in diameter, and the thickenings of the cell-walls, together with the distribution of the pits, are essentially the same as in the *Leucolejeunea*.

MASTIGOLEJEUNEA AURICULATA (Wils. & Hook.) Schiffn. The genus *Mastigolejeunea* agrees with the preceding genus in having the shoot differentiated into a primary caudex attached to the substratum and secondary stems. The latter spread very slightly, and the plants in consequence form depressed mats. The pigmentation is sometimes so pronounced that both leaves and axial organs appear almost black when dry. The stems branch irregularly and the branches, in many cases, give rise to secondary and tertiary branches, all essentially like the stem. The range of the common *M. auriculata*, which grows on trees, logs, and rocks, extends from Florida to Louisiana and southward through the tropics of North and South America. The stems are mostly 3–5 cm. in length by 0.15–0.18 mm. in diameter, and the cell-walls in cross-section are pigmented throughout with varying shades of yellow or brown. Usually, however, a dark brown band one or two cells wide can be distinguished along the ventral edge of the section and a paler brown, more indistinct band along the dorsal edge.

The cortex, as seen in a cross-section (fig. 4, B), is clearly differentiated from the medulla. The cortical cells, which number fifteen to eighteen, measure 15–25μ in width by 15–20μ in thickness, and the dorsal cells tend to be larger than the ventral. The cells show considerable variation, not only in size, but also in the thickness of their walls. The external walls of the dorsal and lateral cells in the figure, for example, are 4–6μ thick, and the cavities are fairly large; but a group of ventral cells is shown with walls 8μ thick and much smaller cavities, which tend to be slit-like. Similar cells are present in most cross-sections. They are normally ventral in position but may extend for variable distances up the sides. The thick walls are further characterized by their distinct middle lamellae, which are darker than the other layers.

The medulla is mostly six or seven cells across and is composed of thick-walled cells having an average diameter of about 13μ. Adjoining the cortical cells with the thickest walls there is usually a group of similar medullary cells with uniformly thickened walls and distinct middle lamellae. The other medullary cells have walls almost as thick but the thickenings, owing to the presence of numerous pits, present the appearance of being formed by the coalescence of robust trigones. The thickness of the wall between two medullary cells is usually between 6μ and 8μ but may be as much as 10μ.

Macerated preparations of the stems bring out a few additional features of the component cells. The cortical cells, two groups of which are represented in surface-view, are mostly 25–60μ in length. The seven partially separated cells shown in figure 4, C, have relatively thin radial

walls, and the three cells shown in figure 4, D, relatively thick radial walls. The cells in both groups have thin end-walls and are destitute of pits in the radial walls. The ends of the cells show little evidence of overlapping. The medullary cells are mostly 70–200μ in length and show a tendency to be shorter in the vicinity of the cortex than in the interior. Figure 4, E–I, represent cells from a more or less peripheral position. These cells have uniformly thickened longitudinal walls and, in most of the examples, thin end-walls. In some cases the broad, transverse or oblique ends lack outgrowths of any kind, but the cell shown in figure 4, G, has two short solid processes at the lower end, and the cell shown in figure 4, F, has two thin-walled protuberances at the upper end. Apparently the longitudinal walls are destitute of pits. The cells represented in figure 4, J–N, are from the interior of the medulla. These cells are mostly longer than the peripheral cells and each one shows one or more pits in optical section; otherwise they present no distinctive features. The old cell shown in figure 4, M, has the lumen bridged across in several places by thin films of cell-wall substance, and one of the pit-canals on the left-hand side has been filled up in the outer part, leaving a small cavity next to the pit-membrane. A similar condition has been noted in *Ptychanthus striatus*.

THYSANANTHUS AMAZONICUS (Spruce) Schiffn. The genus *Thysananthus* is closely related to *Mastigolejeunea* and agrees with it in general habit. In other words the plants form depressed mats and are differentiated into prostrate primary stems, adherent to the substratum, and free, irregularly branched secondary stems. The genus, although largely paleotropic, has a few representatives in tropical America; and *T. amazonicus*, according to Spruce, is perhaps the most abundant of all the Lejeuneae along the Amazon and its tributaries. The plants are brownish, except the young bright green tips, and grow on the branches and trunks of shrubs and small trees. The secondary stems are mostly 3–8 cm. in length by about 0.15 mm. in diameter, and cross-sections show an orange brown pigmentation, which is uniform except for the indistinct and slightly darker middle lamellae. These are not represented in the section illustrated (fig. 4, O). The cortex, as shown in the figure, is not sharply demarcated from the medulla. It is composed of thirty to thirty-three rows of thick-walled cells, 10–20μ in width by 10–15μ in thickness, and the external walls are mostly 4–7μ thick. The medulla, which is eight to ten cells across is composed of thick-walled cells about 13μ in diameter. The walls, in many cases, are as much as 6–8μ thick, but the cell-cavities are distinctly larger than those of the cortical cells. The medulla, in consequence, appears a little more open than the cortex. Owing to the rather numerous

pits in the medulla, the thickenings of the walls, in some cases at least, seem to be formed by the coalescence of trigones, much as in *Leucolejeunea xanthocarpa* and *Archilejeunea Spruceana*.

In young stems the cortex is more sharply marked off from the medulla than in mature stems. A cross-section (fig. 4, P) shows this clearly and indicates further that the differentiation of the tissues progresses centripetally from the periphery toward the interior. In the section represented the walls of the cortical cells have already received deposits of thickening, although the process has not yet come to an end. The medulla, however, is still composed of thin-walled cells, with the exception of the peripheral layer, and even here the process of thickening is still in its early stages.

BRACHIOLEJEUNEA INSULARIS Evans. In the species so far considered the disparity in size between the cortical and medullary cells, as seen in cross-sections of stems, has been comparatively slight. In most cases, to be sure, the cortical cells have been a little larger than the adjoining medullary cells, but they have been approached or even equaled in size by some or all of the interior medullary cells. In other cases, where the medullary cells have been uniform throughout, there has been almost no difference in size between the cortical and medullary cells; and, in a very few cases, the cortical cells have been a little smaller than the medullary cells. In *Brachiolejeunea insularis* and in a few other Holostipae now to be discussed, the cortical cells, in cross-section, are distinctly larger than the medullary cells. The stems of these species agree in most respects with the first type of stem-structure distinguished by Herzog (1925, p. 67), who looks upon the large-celled cortex as a water-storage tissue. It probably plays an important part also in photosynthetic processes, as suggested by Buch (1932, p. 57, footnote).

The genus *Brachiolejeunea* has numerous representatives in tropical regions throughout the world, and a few species are found in subtropical or even temperate localities. The plants, which are usually deeply pigmented, form depressed mats, and the prostrate stems are irregularly branched. According to our present knowledge *B. insularis* is restricted to the West Indies, where it grows on either trees or logs. The stems, in well-developed specimens, are 6–10 cm. long and about 0.16 mm. in diameter. In cross-sections the cell-walls everywhere have a uniform pale yellow or cream color, with the frequent exception of the outermost walls, which may be a pale yellowish brown. The cortical cells (fig. 5, A), fourteen to sixteen in number, are rectangular to subquadrate and measure 25–40μ in width and thickness. They are distinguished by their large cavities and

relatively thin walls, those on the outside being only 1–3μ in thickness. The medulla is six or seven cells across, and the medullary cells average about 17μ in diameter. The walls of these cells, which are essentially alike throughout the section, are about 4μ thick, with more pronounced thickenings at the angles, and an occasional pit can be demonstrated.

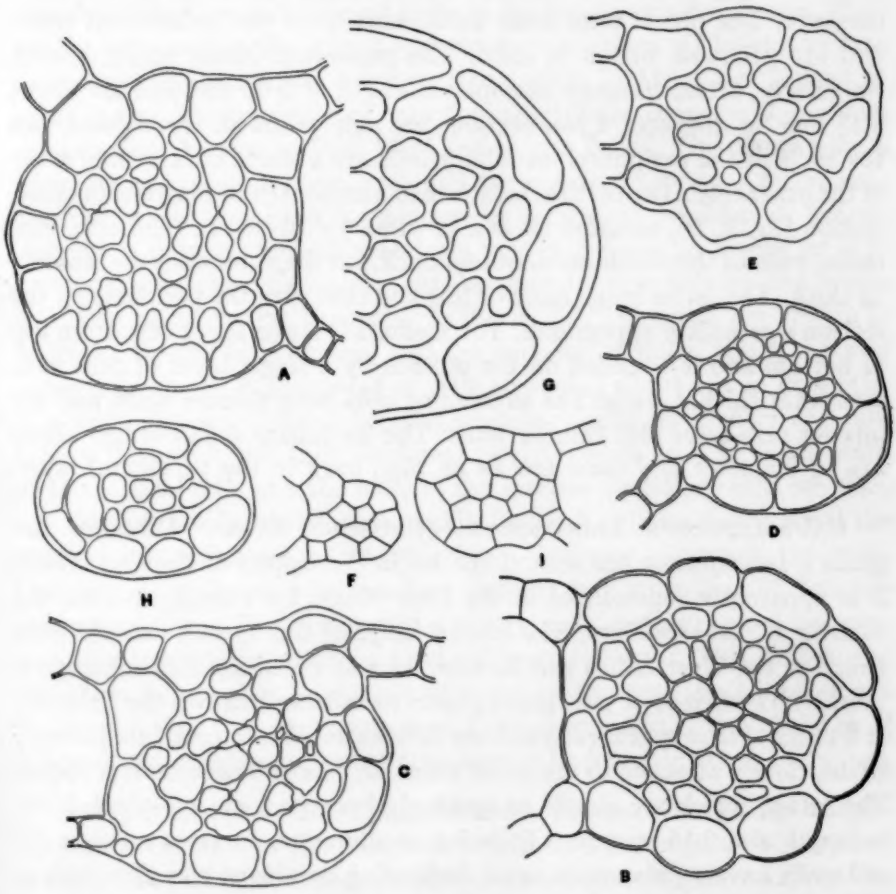


Fig. 5. Cross-sections. A. Stem of *Brachiolejeunea insularis* Evans, leaf attached at right, lobe of another leaf at left. B. Stem of *Dicranolejeunea axillaris* (Nees and Mont.) Schiffn., leaf attached at left. C. Stem of *Caudalejeuna Lehmanniana* (Gottsche) Evans, leaf attached at left, lobe of another leaf at right. D. Stem of *Odontolejeunea lunulata*, leaf attached at left. E, F. *Anoplolejeunea conferta* (Meissn.) Evans. E. Stem, leaf attached at left. F. Microphyllous branch, leaf attached at left. G. Stem of *Cyclolejeunea chitonia* (Tayl.) Evans, lateral half. H. Stem of *C. peruviana* (Lehm. and Lindenb.) Evans. I. Stem of *C. convexistipa* (Lehm. and Lindenb.) Evans, leaf attached at right. All, ×225.

DICRANOLEJEUNEA AXILLARIS (Nees & Mont.) Schiffn. The genus *Dicranolejeunea* is widely distributed in the tropical regions of both Hemispheres. In some of the species the plants are prostrate throughout; in others a differentiation into a prostrate primary stem and spreading secondary stems is met with. The species under consideration, which is found in many parts of North and South America, belongs in the latter category. The plants form loose tufts, usually on the branches of trees, and are yellowish brown in color. The secondary stems, which branch irregularly, attain in many examples a length of 5–10 cm. and are about 0.15 mm. in diameter. Cross-sections are pale yellowish throughout, but the walls of the peripheral medullary cells are a shade darker than those of the other cells. The cortical cells, which number ten to fourteen in cross-section (fig. 5, B), measure 30–60μ in width by 20–30μ in thickness. The radial walls of these cells are about 4μ thick, but the outer walls are scarcely 2μ thick. The latter bulge more or less and thus give the periphery of the section a crenulate appearance. The medulla is six or seven cells from top to bottom and is bounded on the outside by a single layer of cells with somewhat thicker walls. The succeeding cells have thinner walls and the interior cells have still thinner walls. The medullary cells average about 17μ in diameter and show few or no pits, even in the peripheral layer.

CAUDALEJEUNEA LEHMANNIANA (Gottsche) Evans. Although the genus *Caudalejeunea* has several species in the tropics of the Old World, it is apparently represented in the New World by a single species, the variable *C. Lehmanniana*. The known range of this species extends from Brazil to the West Indies and Mexico, with an extension into subtropical Florida. The bright or pale green plants form loose tufts on the branches and twigs of trees and shrubs and are differentiated into prostrate primary stems, closely attached to the substratum, and spreading secondary stems. The latter, which are simple or sparingly branched, are mostly 2–3 cm. in length and 0.15 mm. or a little less in diameter. In cross-sections the cell-walls have a pale cream color, indicating an almost complete lack of pigmentation. The cortical cells (fig. 5, C), about twelve of which are present in each section, are mostly 30–40μ in width by 20–30μ in thickness. Their walls are slightly thickened, up to perhaps 4μ, but in many cases the radial and inner tangential walls show thin places. The medulla is five or six cells across, and the medullary cells average about 18μ in diameter. The walls of these cells are nearly or quite as thick as those of the cortical cells, at least in well-developed stems, but the thickenings at the angles of the cells are more pronounced than along the sides. The wall-

thickenings, in fact, give the effect of coalescent trigones, except where pits are present.

ODONTOLEJEUNEA LUNULATA (Web.) Schiffn. Although most of the preceding species have been epiphytes, they have grown on the trunks or branches of trees or shrubs. Many of the *Odontolejeuneae*, however, are strictly epiphyllous in habit and grow on the upper surface of leaves. They are, in fact, among the largest and most conspicuous of the epiphyllous Lejeuneae. The genus has a few representatives in Africa but is most at home in the American tropics, and the range of the common *O. lunulata* extends from Mexico and the West Indies into Brazil. The plants have a brownish or yellowish green color and grow closely appressed to the substratum, where they form flat patches, sometimes of considerable extent. The stems branch irregularly and are mostly 2–5 cm. in length by 0.15 mm. or a little less in diameter. Cross-sections are very pale grayish brown and show about twelve cortical cells (fig. 5, D). The latter are 25–35μ in width by 20–30μ in thickness, and the enclosed medulla, which is six or seven cells across, is composed of cells averaging about 13μ in diameter. The walls of the peripheral layer of medullary cells are slightly and uniformly thickened, but their thickness rarely exceeds 4μ. The radial walls of the cortical cells and the walls of the interior medullary cells are thin, but the outer walls of the cortical cells (at least in some cases) equal the walls of the peripheral medullary cells in thickness. Although the stem-structure of *O. lunulata* agrees in a general way with that of *Brachiolejeunea insularis*, *Dicranolejeunea axillaris*, and *Caudalejeunea Lehmanniana*, it is more delicate, owing to the thinner cell-walls. This evidence of reduction is probably associated with the epiphyllous habit, and it will be shown below that the epiphyllous Lejeuneae include some of the most reduced and simplified types of structure to be found in the entire group.

ANOPLOLEJEUNEA CONFERTA (Meissn.) Evans. The genus *Anoplolejeunea* is confined to the American tropics and is composed of very few species. The plant under consideration forms depressed green mats on the bark of trees and has an extensive range in both North and South America. The prostrate stems, which branch irregularly, are mostly 3–5 cm. in length and have a diameter of 0.12–0.17 mm. Some of the branches cling to the substratum and agree with the stem in having large leaves, but others are ascending and microphyllous. The stems show a pale and uniform brownish yellow pigmentation of the cell-walls in cross-sections. The cortical cells, as in the four preceding species, are distinctly larger than the medullary cells. Instead of being arranged, however, in ten to sixteen longitudinal rows, they are arranged in seven longitudinal rows. Of these

rows two are ventral in position, two on each side lateral and one dorsal. The illustration (fig. 5, E) shows the seven rows clearly in cross-section, but an additional cell is present on the left-hand side, marking the place of attachment of a lobule. The arrangement of the cortical cells in seven longitudinal rows and the distribution of these rows around the stem in the manner just described are unusual in the Holostipae but are found with few exceptions throughout the Schizostipae and also in the genera of the Paradoxae with underleaves. The significance of this arrangement and particularly of the dorsal row of cells will be considered later, in connection with the development of the stem.

The cortical cells of the *Anoplolejeunea* measure 40–50μ in width by 25–35μ in thickness, and some of the cells bulge slightly, thus giving the section an irregular contour. The walls are uniformly thickened, and the external tangential walls have a thickness of 6–8μ. The medulla is about four cells across, and the medullary cells have an average diameter of about 20μ. Their walls may be as much as 6μ thick, and the triangular thickenings at the angles are more or less distinct. The section figured does not show pits clearly, but these structures can occasionally be demonstrated, not only in the walls between medullary cells, but also in the walls between medullary and cortical cells.

The microphyllous branches are much more slender than the stems and branches with normal leaves and measure scarcely 0.05 mm. in diameter. Although seven rows of cortical cells are present, just as in the stem, the medulla is greatly reduced, and only three or four cells appear in cross-sections. When only three cells are present, as in the section shown (fig. 5, F), one is ventral in position and two dorsilateral, with the dorsal cortical cell fitting in between them. The cortical cells are 15–20μ in width and thickness and the medullary cells about 10μ in diameter. All the walls are thin, except for the occasional presence of minute triangular thickenings at the angles of the medullary cells.

Schizostipae

CYCLOLEJEUNEA CHITONIA (Tayl.) Evans. The genus *Cyclolejeunea* is here placed among the Schizostipae, in spite of the fact that the underleaves, at least in certain species, may be undivided. The genus is predominantly neotropical, but two species from Java have recently been assigned to it. In the West Indian *C. chitonia*, the first species to be considered, the plants form depressed mats of an olive green or brownish color on the bark of trees or on logs. The prostrate stems branch irregularly and are mostly 2–5 cm. in length by about 0.25 mm. in diameter. Cross-sections show a pale brownish yellow pigmentation, with little variation

in shade. About twelve cortical cells appear in each section, and these cells, which are unusually large, measure 40–60μ in width by 25–40μ in thickness (fig. 5, G). The outer walls are 8–10μ thick; the radial walls are a little thinner, and some of them show more or less distinct pits. The medulla, which is seven or eight cells across, is composed of cells about 20μ in diameter. The walls of the medullary cells are all thickened, but a gradual decrease in thickness is apparent in passing from the peripheral layers, where the walls are 6-8μ thick, to the interior, where the walls are only 2–4μ thick, except at the angles of the cells. Pits can be demonstrated here and there in the medulla.

CYCLOLEJEUNEA PERUVIANA (Lehm. & Lindenb.) Evans. The plants of *C. peruviana* are epiphyllous in habit and form irregular reddish brown patches. The species is abundant in the valley of the Amazon and adjoining regions and ascends into the foothills. It is frequently associated with *Odontolejeunea lunulata* and other *Odontolejeuneae* and rivals them in size. The stems, which cling closely to the substratum, branch irregularly and are mostly 3–5 cm. in length. They measure 0.11–0.14 mm. in width and 0.08–0.1 mm. in thickness, thus showing a slight dorsiventral compression. Cross-sections are of a uniform pale yellow color and normally have seven cortical cells, just as in *Anoplolejeunea conferta*, but in the section illustrated (fig. 5, H) the lower lateral cell on the left seems to have undergone a division by means of a thin radial wall. This wall, however, is really oblique and separates two cells of the same longitudinal row. The cortical cells are 30–40μ in width by 20–30μ in thickness and have walls about 6μ thick, with thinner areas in the radial walls. The medulla, in contrast of that of the more robust *C. chilonia*, is only three or four cells across. The cells average about 15μ in diameter, and their walls are about as thick as those of the cortical cells.

CYCLOLEJEUNEA CONVEXISTIPA (Lehm. & Lindenb.) Evans. The range of this species, which is perhaps the most abundant of all the epiphyllous Lejeuneae, includes the greater part of tropical America. The plants, which are more delicate than those of *C. peruviana*, form irregular pale green patches, and the cell-walls are scarcely if at all pigmented. The prostrate stems are mostly 1–2 cm. in length by 0.08 mm. in diameter and branch copiously and irregularly. Some of the branches are much like the stem, but the gemmiparous branches, which are ascending to suberect, bear modified leaves and underleaves. The cortical cells (fig. 5, I) are definitely in seven longitudinal rows and measure 25–35μ in width by 15–20μ in thickness. The medulla is three or four cells across and is composed of cells av-

eraging about 11μ in diameter. All the cell-walls are thin, except in some cases those of the cortical cells, which may be slightly thickened.

POTAMOLEJEUNEA ORINOCENSIS Steph. This aquatic species is one of the very few Schizostipae known to the writer in which the cortical cells are arranged in more than seven longitudinal rows. The pale green plants

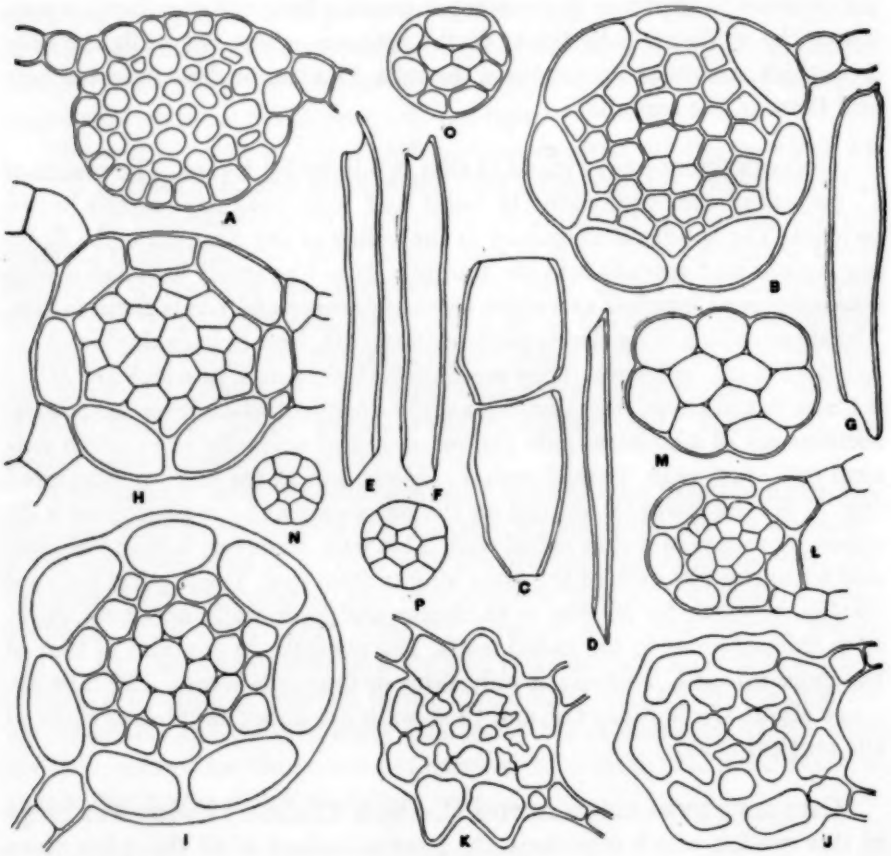


Fig. 6. Cross-sections of stems, except C–G. A. *Potamolejeunea orinocensis* Steph., a lobe attached on each side. B–G. *Taxilejeunea pterogonia* (Lehm. and Lindenb.) Schiffn. B. Lobe attached at right. C. Two cortical cells. D–G. Medullary cells. H. *Hygrolejeunea cerina* (Lehm. and Lindenb.) Schiffn., leaf attached at left. I. *Cystolejeunea lineata* (Lehm. and Lindenb.) Evans, underleaf attached at left. J. *Euosmolejeunea trifaria* (Nees) Schiffn., leaf attached at right. K. *Pycnolejeunea macroloba* (Mont.) Schiffn., leaf attached at right and lobe of another leaf at left. *L. Lejeunea flava* (Swartz) Nees, leaf attached at right. M. *L. inundata* Spruce. N. *Microlejeunea bullata* (Tayl.) Evans. O. *Drepanolejeunea inchoata* (Meissn.) Schiffn. *P. Leptolejeunea elliptica* (Lehm. and Lindenb.) Schiffn. All, ×225.

form loose tufts on moist rocks in the lowlands of tropical South America and are often completely submerged. The stems, which are about 0.12 mm. in diameter, give off branches at fairly regular intervals and may attain, according to Stephani, a length of 12 cm. Cross-sections are colorless or a very pale cream color and cut through about twenty cortical cells, which measure 10–20μ in width and thickness (fig. 6, A). The thin outer walls of these cells bulge more or less and give the section a crenulate contour. The radial walls also are thin toward the outside but thicken slightly toward the medulla. The cells of the latter are in about six layers and average about 16μ in diameter. Their walls are about 4μ thick, and the thickening is uniform, except for the fact that the cavities are rounded. Pits are difficult to demonstrate, but the middle lamellae show clearly in many of the walls.

TAXILEJEUNEA PTEROGONIA (Lehm. & Lindenb.) Schiffn. In this widely distributed species of tropical America, the differentiation of the stem-tissues and the arrangement of the cortical cells in seven longitudinal rows are exhibited with almost diagrammatic distinctness. The plants are pale green and form loose mats on rocks and firm soil. The stems are mostly 3–4 cm. long by 0.15–0.2 mm. in diameter and give off a few long vegetative branches in addition to the short sexual branches. Cross-sections show a complete lack of pigmentation in the cell-walls. The large cortical cells (fig. 6, B) are 40–60μ in width by 20–30μ in thickness, and their walls are about 4μ thick. The bounding walls bulge outward and the inner tangential walls bulge inward. The circumference of the section, in consequence, appears more or less crenulate and the periphery of the medulla more or less stellate. The latter is seven or eight cells across, and the medullary cells average about 14μ in diameter. The walls between the cortex and medulla are about 6μ thick and those of the peripheral medullary cells about 4μ thick. In passing inward the walls become thinner and thinner, and the interior cells are thin-walled. Neither middle lamellae nor pits show in cross-sections.

It is perhaps worthy of note that a vertical line passing through the dorsal cortical cell and between the two ventral cortical cells divides the section into symmetrical halves. This indicates that the stem is a bilaterally symmetrical organ with respect to a median vertical plane of symmetry, if a horizontal position is assumed. The vertical line, however, is not the only axis of symmetry. A line passing through any cortical cell and between the opposite pair of cortical cells would likewise be an axis of symmetry. Since seven cortical cells are present the section would have

seven axes of symmetry and the stem seven planes of symmetry. This indicates that the stem, considered by itself, is really a radial organ.

Macerated preparations show that the cortical and medullary cells, in their essential features, are in agreement with those of some of the Holostipae already considered. The cortical cells (fig. 6, C) are mostly 50–90μ long and fit together with blunt angles. In some of the cells the ends overlap slightly or give off one or two short and blunt projections, but such features are not strongly in evidence. The end walls remain thin; but the longitudinal walls, as already noted in the cross-sections, are uniformly thickened, and pits are conspicuous by their absence. In figure 6, D–G, four medullary cells are represented, and the cell shown in figure 6, G, is nearer the interior than the others. These cells are mostly 150–190μ in length, their end walls are mostly thin, and their longitudinal walls uniformly thickened. The ends of the cells vary from transverse to oblique; and, in some cases, one or two short projections are present. Even in the thickest longitudinal walls no pits are visible.

HYGROLEJEUNEA CERINA (Lehm. & Lindenb.) Schiffn. The species of the tropical genus *Hygrolejeunea* are similar to the Taxilejeuneae and, in some cases at least, form depressed mats. In *H. cerina*, a widely distributed species of Brazil and the West Indies, the pale green, sparingly branched plants grow on the branches of trees and shrubs and may be as much as 5 cm. in length. The stems are about 0.12 mm. in diameter and are similar in structure to those of *Taxilejeunea pterogonia*, except that the medulla is less differentiated and relatively smaller. The cell-walls in cross-sections appear colorless or a pale cream color. The cortical cells (fig. 6, H), seven in number, are mostly 40–60μ in width by 20–30μ in thickness, and their slightly bulging bounding walls are about 4μ thick. The radial walls and the walls between the cortex and medulla equal or slightly exceed the bounding walls in thickness and may be as much as 6μ thick. The medulla is four to six cells across and is composed of cells about 20μ in diameter. The radial walls of the peripheral layer are slightly thickened in the vicinity of the outer tangential walls, but the thickness diminishes rapidly toward the center of the stem, and the inner portions of the radial walls, together with all the walls of the interior medullary cells, are thin.

CYSTOLEJEUNEA LINEATA (Lehm. & Lindenb.) Evans. The genus *Cystolejeunea* is monotypic and its single species, *C. lineata*, is widely distributed in the West Indies, forming pale green depressed mats on trees or growing in admixture with other hepatics. The stems, which give off occasional branches, are about 0.15 mm. in diameter and may attain a length

of 5 cm. or even a little more. Cross-sections show a uniform, pale yellowish brown pigmentation. In its general features the anatomical structure of the stem is much like that of the two preceding species. It shows, in other words, a differentiation into a cortex composed of large cells in seven longitudinal rows and a medulla composed of smaller cells. The cortical cells (fig. 6, I) are 45–60μ wide by 30–40μ thick, and their bounding walls are mostly 8–10μ in thickness. The radial walls and the walls between the cortex and medulla are nearly or quite as thick as the bounding walls. The medullary cells are in five or six layers and average about 19μ in diameter. Except for the outer tangential walls of the peripheral cells, the walls of the medullary cells are thin or only slightly thickened. All the cells, however, show triangular thickenings at the angles, and these may coalesce.

EUOSMOLEJEUNEA TRIFARIA (Nees) Schiffn. The genus *Euomolejeunea* is predominantly tropical, but a few of the species extend into subtropical or temperate regions. Most of the species are yellowish green in color, and many have a more or less pronounced odor. In *E. trifaria*, which is found in most tropical countries throughout the world, the plants form depressed mats on trees. The sparingly branched stems may be 5 cm. or more in length, and the example sectioned was 0.13 mm. wide and 0.11 mm. thick, thus showing a slight dorsiventral compression. The cell-walls in cross-sections are pale yellow throughout. The seven cortical cells (fig. 6, J) are mostly 35–50μ in width by 20–30μ in thickness, and the walls are 8–10μ thick. The outer walls, which bulge more or less, may be bluntly angled, and the periphery of the section in consequence appears crenulate or denticulate. The medulla is about four cells across and its cells average about 20μ in diameter. These cells are all thick-walled, and the walls between the medulla and cortex may be nearly or quite as thick as the walls of the cortical cells; the walls between the medullary cells are a little thinner but show more or less distinct triangular thickenings at the angles. In a few of the walls pits can be demonstrated. Except for the fact that the cell-walls are everywhere thickened, the anatomy of the stem in *Euosmolejeunea trifaria* is much like that of the three preceding Schizostipae.

PYCNOLEJEUNEA MACROLOBA (Mont.) Schiffn. The densely imbricated leaves in *Pycnolejeunea* will serve to distinguish the genus from most of the other Lejeuneae Schizostipae. The species are found in most tropical regions, and a few occur in Chile and Australasia. In the tropical American *P. macroloba* the plants form compact depressed mats on the bark of trees and have a yellowish or yellowish brown color. The stems, which give off a few irregular branches, are mostly 2.5–3.5 cm. in length by 0.09–0.1 mm.

in diameter and appear cream color in cross-sections. Although the cortical cells show the usual arrangement in seven longitudinal rows, most cross-sections have one or two additional cortical cells (fig. 6, K), owing to the crowding together of the leaves and underleaves. The cells in question, which are mostly 25–30μ in width by 20–35μ in thickness, bulge strongly and may even form bluntly angled projections. This is especially true of the two ventral rows. The walls of the cortical cells are about 6μ thick, and pits can be demonstrated in some of the radial walls. The medulla is composed of three or four layers of cells which average about 15μ in diameter. Their walls equal in thickness the walls of the cortical cells, except where pits are present, and these occur not only in the walls between medullary cells but also in the walls between medullary and cortical cells.

LEJEUNEA FLAVA (Swartz) Nees. The generic name *Lejeunea* is here retained for the group of species to which *L. cavifolia* (Ehrh.) Lindb. belongs. It is one of the largest and most widely distributed genera of the Schizostipae, and its range extends to rather high northern and southern latitudes, although the majority of the species are tropical. *L. flava* is perhaps the most widely distributed of all and is found not only in the tropics of both Hemispheres but also in Ireland and the southern United States. The pale green or yellowish green plants are delicate in texture and form depressed mats or thin patches on the bark of trees, on rocks, or even on living leaves. The stems, which branch sparingly and irregularly, show a cream color in cross-sections. They are mostly 1–5 cm. in length by 0.07–0.08 mm. in diameter; and their cortical cells, which show the characteristic arrangement in seven longitudinal rows, measure 25-30μ in width by 15–20μ in thickness (fig. 6, L). The bounding walls of these cells are thin, but the radial walls and the walls between the cortical and medullary cells may be thickened, although their thickness rarely exceeds 6μ. The medulla is mostly four cells across and the cells average about 12μ in diameter. The walls, in some cases, show minute triangular thickenings at the angles of the cells but are otherwise thin throughout.

LEJEUNEA INUNDATA Spruce. The taxonomic position of this aquatic species, which grows on rocks and on branches of trees in the lowlands of Brazil and adjacent regions, is not altogether certain. Spruce placed it in his subgenus *Eu-Lejeunea*, the equivalent of the genus *Lejeunea* as here restricted, but Stephani transferred it to the genus *Potamolejeunea*. The cortical cells of the stem, however, instead of being arranged in numerous longitudinal rows as in *P. orinocensis*, are arranged in only seven longitu-

dinal rows, thus conforming to the usual arrangement found in the Schizostipae. For this reason the species is here retained in *Lejeunea*, although the medulla is more simply organized than in *L. flava*. The medullary cells, in fact, are arranged in only three longitudinal rows. The irregularly branched stems, the cell-walls of which are unpigmented throughout, are mostly 5–7 cm. in length, 0.08–0.1 mm. in width, and a trifle less in thickness. The cortical cells measure 20–30μ in width and thickness and bulge more or less, thus giving the cross-sections a crenulate appearance (fig. 6, M). The outer cell-walls are 3–4μ thick, but the radial and inner tangential walls are thin. The medullary cells average about 25μ in diameter and are thin-walled, except for the more or less pronounced triangular thickenings at the angles.

Simplified types of stem-anatomy, similar to that just described, are to be found in numerous epiphytic Lejeuneae and especially in species that are epiphyllous in habit. Characteristic examples of these will now be considered, and it will be shown that the process of simplification or reduction in certain Paradoxae has progressed even farther than in *L. inundata*.

MICROLEJEUNEA BULLATA (Tayl.) Evans. The genus *Microlejeunea* includes some of the most delicate and inconspicuous of the Lejeuneae. Most of the species are tropical, but a few are found in subtropical or temperate regions. The slender pale green plants of *M. bullata*, which is widely distributed in tropical America as well as in Florida, usually grow scattered on the bark of trees, in many cases mixed with other hepatics. The stems, which branch sparingly, are only 2–3 mm. in length by about 0.03 mm. in diameter. Although seven rows of cortical cells and three rows of medullary cells are present (fig. 6, N) just as in *L. inundata*, the cells are smaller and thin-walled throughout. The cortical cells, for example, are only 6–10μ in width and thickness, and the medullary cells only 4–5μ in diameter. All the cell-walls are unpigmented.

DREPANOLEJEUNEA INCHOATA (Meissn.) Schiffn. The large genus *Drepanolejeunea*, which is predominantly tropical in its distribution, includes both corticolous and epiphyllous species. The neotropic *D. inchoata* belongs to the latter category and grows in irregular pale green patches. The sparingly pinnate stems are mostly 0.5–1 cm. in length by 0.05–0.06 mm. in diameter and agree with the two preceding species in the number and arrangement of the cortical and medullary cells. As seen in cross-section (fig. 6, O) the seven cortical cells are 20–30μ in width by 15–20μ in thickness, and the three medullary cells average about 12μ in diameter. The

unpigmented cell-walls are 2–3μ in thickness, with the exception of the still thinner walls separating the medullary cells from one another.

LEPTOLEJEUNEA ELLIPTICA (Lehm. & Lindenb.) Schiffn. The tropical and subtropical genus *Leptolejeunea* is composed largely, if not entirely, of epiphyllous species, which form irregular pale green patches. The pinnate or bipinnate stems of *L. elliptica*, which is widely distributed in the American tropics, are mostly 0.5–1 cm. long and 0.04 mm. in diameter. The colorless cross-sections (fig. 6, P) are essentially like those of *Microlejeunea bullata*, except that the cells are somewhat larger. The cortical cells, for example, measure 10–15μ in width and thickness, and the medullary cells average about 10μ in diameter.

(*To be concluded*)

A new species of Collybia from Connecticut

PAUL W. GRAFF

(WITH PLATE 13)

While recently tramping through an old wood's road in Storrs, Connecticut, my attention was attracted by a young colony of *Collybia* apparently just beginning to produce its first crop of pilei. But four or five young caps were found at that time, though there were very evident indications of a prospective colony of some size. A considerable gray-white mycelial growth was present among decaying woody remains in the soil of the roadway. In view of the apparent possibilities, the locality was revisited the next day, and visits were continued during the subsequent development of the fungus.

This *Collybia* was growing on a corduroy section of an old roadway winding through young mixed, deciduous woods. The young growth is approximately a twenty-five year old stand on the site of an older timbered area. The corduroy material was partly decayed, and to some extent covered with soil in which a few grasses and low weeds were growing. It was evident that the woody substrate was an important factor in the development of the fungus. Though shaded a goodly portion of the day, this section of the road received sunlight for two or three hours during the afternoon. The soil, for some distance about, contained considerable moisture, held by a rich, deep humus. There is a spring and a small swamp in the vicinity which aids in maintaining this moisture supply.

The development of the colony was rapid. The next afternoon eighteen pilei were present, all of which were fully expanded. These were in three clusters, with a few scattered individuals near. Two days later the number of clusters had materially increased, but those previously seen had disappeared, for the most part, leaving only a few decaying remnants. The number of pilei present at this time was much greater, and the clusters larger. In one alone were nine fully matured and closely overlaying caps.

While closely gregarious, in no case was this species found to be truly caespitose, though many members of this genus have that habit. It was also of interest to note that when visited at any time during the afternoon none but fully expanded pilei were found. Hot weather was continuous through the period of these observations. Development from the pilear initials seems to have taken place during the cooler night and early morning hours, to be followed by a brief period of maturity. Early insect attack was the rule, and by mid-afternoon all pilei were thoroughly infested.

On this same day, for some distance from the original colony, scattered individuals were found in the adjacent woods. These appeared in all

cases as solitary pilei. None of the gregarious habit, so pronounced in the material of the road, was to be seen in this habitat. As compared with the other specimens, those of the woods had pilei of relatively lesser diameter. They also had longer and more slender stipes. In color and all other characteristics, however, they appeared identical. The soil of the woods at this place was particularly rich in decaying twigs and branches.

Upon visiting the locality two days later, five days after the plants were first observed, not a single growing individual was to be found, either in the roadway or in the woods. The only clue indicative of the presence of the fungus was one insect infested cap in an advanced state of decay. Subsequent visits to the place during the next two weeks were fruitless. The vigorous rapid development had seemingly been followed by sudden obliteration. Both humidity and temperature were high during this period. The general conditions prevailing were such as to remind one of the difficulties attendant upon the collection and preservation of fleshy fungi in the tropics.

When young the caps of this species open out hemispherically, but soon expand. In doing so they usually become first somewhat umbonate, then irregularly flattened, with sometimes a retention of the central umbo but frequently slightly depressed in the center, due to the raising of the surrounding portion. The margin is frequently irregular as it may be in part slightly repand while other portions are extended or slightly inrolled. This condition is most likely to be found in the clustered forms where some pilei overlap others. In the case of single isolated individuals these irregularities are not so pronounced, and may be absent. The upper surface of the pileus is glabrous and hygrophanous, in texture much like that of *Collybia dryophila* or *C. platyphylla*. It is never sticky when moist as is *C. velutipes*. When fully expanded the cap varies from 7 to 17 cm., in diameter. Among the open road forms the most usual diameter for mature pilei was found to be 13 cm., while 9 cm. was the most usual for the solitary woodland plants.

When fresh the color of the upper surface is, according to Ridgway's "Color Standards," deep colonial buff at a point half way from margin to center, and slightly lighter toward the margin. The center is darker and agrees with Ridgway's avellaneous. Upon drying it was found that these colors fade considerably. Aside from this, there was very little if any variation in color among the large number of individuals observed.

The flesh of the cap is white, and does not change color upon being bruised. It is of a fine soft texture, characteristically thin, and tapers in thickness from its place of union with the stipe toward the margin. The flesh resembles that of *Collybia dryophila* in consistency and form, but not

in variation of color or relative thickness in proportion to the breadth of gills. The thickness of the flesh, midway stipe and margin, is 3 to 6 mm., usually 5 mm., in the heavier road forms and 4 mm., in those of the woodland.

The gills are notably wider than the flesh of the pileus, and, measured at the same locality, vary from 5 to 10 mm. in width. Here again those of the open road vary from those of the woodland, as the former are usually about 8.5 mm. wide and the latter but 6.5 mm. They are white, but may appear faintly cream colored in mature specimens due to the mass of adhering spores. The gills are very crowded, and their edges are somewhat irregular or slightly serrate. Though the gills of most of our common species of *Collybia* are described as adnate or free, in all examples of this species that I have seen they are adnexed. Interspersed among those of full length are shorter free gills, of varying length, and having full rounded ends toward the stipe. All are narrowed and tapering toward the margin.

The stipe is characteristically cylindrical, but with a well rounded bulbous base. The color of its surface is avellaneous, but of a slightly darker shade than the central portion of the pileus. The interior of the stipe is cartilaginous, stuffed at first, but very soon becoming hollow. The flesh, like that of the cap, does not change color upon being bruised. In the open road forms, whether gregarious or solitary, the stipe varies from 3 to 6 cm. in length, but is usually about 4 cm. in length and 7 mm. thick. As compared with this, the stipe of the woodland form is more slender and longer, usually about 8 cm. in length and 5 mm. in thickness. All forms have a well developed spherical bulb at the base of the stipe. In the open road forms this has a diameter of about 2 cm., while 1.2 cm. is usual for those of the woodland.

The spores are of a very pale creamy tint when mature. Spore prints made upon black paper appear white in color, but when made upon a purely white background this faint creamy tint becomes evident. The average dimension of these spores is $4.2 \times 8.4\mu$. They are not of the ellipsoidal shape most frequently described for members of this genus, but rather are broadly reniform. Upon separation from their sterigmata, the spores are seen to have a short pedicillate appendage of about 1μ in length, by means of which they are attached. The surface of the spores is smooth, and entirely without markings. The basidia are of the typical clavate form, $25–30 \times 5–7\mu$, and interspersed among these are frequent cystidia. These cystidia are quite prominent as they extend some 12 to 15μ beyond the basidia. They are sometimes narrowly obovate or fusiform, but typically ventricose, with a dimension of $38–45 \times 8–10\mu$. The most striking feature of these cystidia is their prominently stellate apices.

Altogether between fifty and sixty pilei of this species were observed during the several days of their production. Due, however, to very early insect attack and the heaviness of this infestation, no satisfactory effort could be made to test their edibility. Maturity was reached very quickly and disintegration followed rapidly. The odor of the fresh pilei is mild and faintly earthy. There is no special attraction from the mycophagist's viewpoint.

The short, heavy-stemmed, broad-capped forms remind one strongly of the genus *Tricholoma* in their general appearance. That genus, however, is typically one of late summer and autumn. Its stipe is of the same substance as the cap, and its gills are notched or sinuate. In gill character *Tricholoma* is intermediate between *Collybia*, on the one hand, and *Mycena* and *Clytocybe*, on the other.

DIAGNOSIS

Collybia sedula sp. nov.

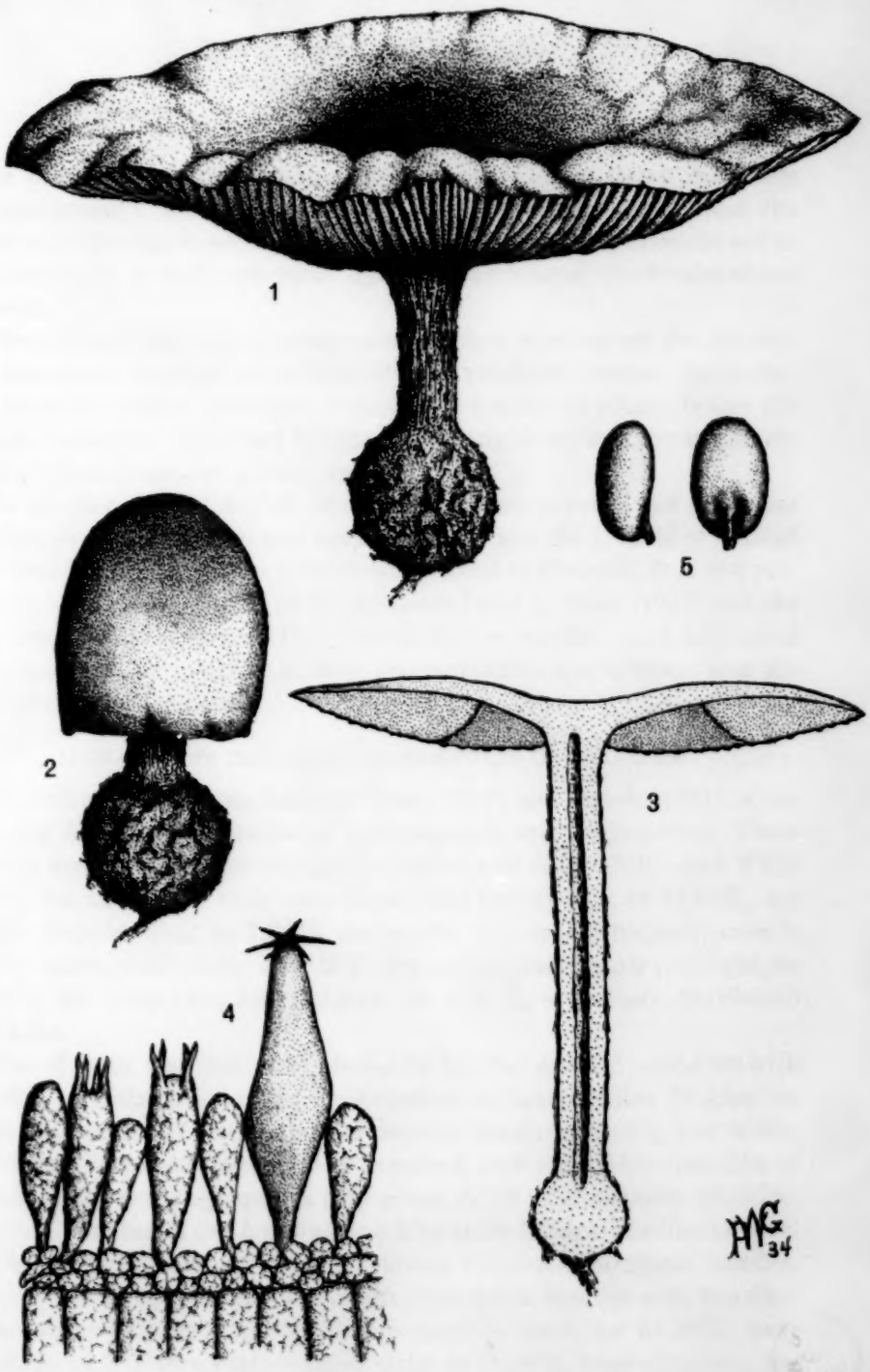
Solitaria vel gregaria; pileo e convexo expanso, primum umbonato, vel omnino expanso, dein convexo-applanato, usque 7–17 cm., (13 cm.) lato; superficie levi, glabra, hygrophana, fulvella, margine pallidiori, centro avellaneo; contextu tenui, albo, 3–6 mm., (5 mm.) lato; lamellis albis, confertis, adnexis, margine sinuati, pluris insertis; stipite recti, cylindrico, arido, fibroso, e farcto cavo, pileo concolor, 3–8 cm., (4 cm.) longis, 0.5–0.7 cm., crassis, basi inflata. 1.2–2.0 cm., diam.; sporis levibus, hyalinis vel pallido-alutaceis, reniformibus, 4.2×8.4μ, pedicillatis; basidia clavata, 25–30×5–7μ; cystidia fusoidea vel fusoideo-ventricosa, 38–45×8–10μ, apice stelliformibus.

Hab. ad terram humosam inter ligna dejecta in silvaticis, Storrs, Tolland County, Connecticut, America Bor., P. W. Graff, 6/21/1934.

Specimens have been deposited in the herbaria of the Connecticut State College, Storrs, Connecticut, and the New York Botanical Garden, Bronx Park, New York City.

Explanation of plate 13

Fig. 1. Young basidiocarp, open road form, natural size.
Fig. 2. Mature basidiocarp, open road form, natural size.
Fig. 3. Section of mature basidiocarp, shaded forest type, natural size.
Fig. 4. Section of hymenium showing basidia and cystidia, ×1000.
Fig. 5. Basidiospores, lateral and inner face as located on the basidium, ×2000.



GRAFF: COLLYBIA SEDULA

The taxonomic and climatic distribution of alkaloids

JAMES B. MCNAIR

In previous papers (McNair 1929–1932) it has been shown that there are relationships between some properties of plant substances and the plants and climates in which they are produced. The study is continued in this article to include vegetable dyes and additional discoveries about alkaloids.

The object of the present study of alkaloids is to bring out the climatic and taxonomic distribution of alkaloids, the relations between the molecular weights, carbon, hydrogen, and oxygen content of alkaloids and the climatic habitats of the plant families producing them; and the specificity of alkaloids as to species, genera, and families.

In another paper (McNair 1931) the relations between the molecular weights, carbon, hydrogen and oxygen content and the climate of habitat were developed with a lesser number (sixty-four) of alkaloids. It is now possible by making use of more of the alkaloids listed by Boas (1927) and the later compilation of Couch (1931) (total 299) to calculate with additional data and probably to arrive at more representative results than those obtained in the earlier article.

CLIMATIC AND TAXONOMIC DISTRIBUTION OF ALKALOIDS

According to the compilation of Boas (1927) and Couch (1931), alkaloids are found in 57 families of gymnosperms and angiosperms. These families are classified climatically by Engler and Gilg (1919), and Willis (1925). An analysis of their data shows that twenty-five, or 43.86%, are mostly tropical; four, or 7.02%, are mostly tropical-subtropical; none is mostly subtropical; three, or 5.26%, are subtropical-temperate; eight, or 14.04%, are temperate; and eighteen, or 31.58%, are widely distributed in habitat.

The climatic distribution of alkaloidal families may be compared with the climatic distribution of the total number of plant families. Making use again of the climatic distribution of these by Engler and Gilg, and Willis, it becomes apparent that of two hundred and ninety-five families of gymnosperms and angiosperms fifty-seven, or 19.32%, contain alkaloids. Of a total number of one hundred and fifty-three tropical families twenty-five, or 16.34%, have alkaloids; of fifteen tropical-subtropical families, four, or 26.6%, have alkaloids; of eight subtropical families none has alkaloids; of seven subtropical-temperate families three, or 63.20%, have alkaloids; of fifty temperate families eight, or 16.00%, have alkaloids, and

fifty-seven families of widely distributed habitats, seventeen, or 29.82%, have alkaloids.

It is evident that of the plant families producing alkaloids three times as many are found in the tropics as in the temperate zone. Those mostly tropical in distribution include 43.86% of all the alkaloid families, while only 14.04% are found growing largely in the temperate zone.

The ratio of tropical alkaloidal families to the total tropical families (16.34%), however, is practically the same as the ratio of temperate alkaloidal families to the total temperate families (16.00%).

The twenty-five tropical alkaloidal families are: Acanthaceae, Aizoaceae, Anonaceae, Apocynaceae, Caricaceae, Cucurbitaceae, Dioscoreaceae, Erythroxylaceae, Hernandiaceae, Lauraceae, Loganiaceae, Loranthaceae, Menispermaceae, Moraceae, Myrtaceae, Palmae, Pedaliaceae, Piperaceae, Rubiaceae, Sapindaceae, Simarubaceae, Stemonaceae, Sterculiaceae, Symplocaceae, and Zygophyllaceae.

The four tropical-subtropical alkaloidal families are: Amaryllidaceae Gnetaceae, Punicaceae, and Theaceae.

No alkaloid-producing family that is largely of subtropical distribution is known.

The three subtropical-temperate distributed alkaloidal families are: Campanulaceae, Nymphaeaceae, and Taxaceae.

The eight alkaloidal families that are mostly temperate in distribution are: Berberidaceae, Cactaceae, Caprifoliaceae, Cruciferae, Papaveraceae, Platanaceae, Ranunculaceae, and Umbelliferae.

The alkaloidal families of widely distributed habitats, of which there are seventeen, are: Aquifoliaceae, Aristolochiaceae, Calycanthaceae, Chenopodiaceae, Compositae, Euphorbiaceae, Fagaceae, Gramineae, Labiatae, Leguminosae, Liliaceae, Malvaceae, Polygalaceae, Rhamnaceae, Rutaceae, Scrophulariaceae, and Solanaceae.

PHYSICAL AND CHEMICAL CONSTANTS IN RELATION TO CLIMATIC DISTRIBUTION

Table 1 brings out certain facts in regard to a probable relationship between climate of habitat and molecular weight, and number of carbon, hydrogen, nitrogen, and oxygen atoms in alkaloids.

Molecular Weights. The maximum and average molecular weights increase markedly from tropical to temperate while the minimum registers a slight decrease.

Carbon Content. The average and minimum number of carbon atoms is the same for both tropical and temperate alkaloids, while the maximum decreases from tropical to temperate.

Hydrogen Content. The minimum and average numbers of hydrogen atoms increase from tropical to temperate, while the maximum numbers indicate a decrease.

Oxygen Content. The maximum, minimum, and average numbers of oxygen atoms increase from tropical to temperate.

Nitrogen Content. Both the average and minimum values for nitrogen are the same in both tropical and temperate families but the maximum decreases from tropical to temperate.

SPECIFICITY OF ALKALOIDS

Of the five families of gymnosperms two, or 40%, have alkaloids. This is a larger proportion than in the angiosperms. Of these, the forty-five families (Willis) of monocotyledons five, or 11.1%, have alkaloids while of the two hundred and forty-one families (Willis) of dicotyledons forty-four, or 18.2%, have alkaloids. The average molecular weights of these are: cryptogams 309, gymnosperms 417, and angiosperms 396.

The alkaloids found in a single plant generally have the closest chemical relationship to each other. Frequently they form a homologous series, often they are isomers, and sometimes stereoisomers. In other instances the difference between these compounds is only in the quantity of hydrogen or oxygen which they possess; accordingly reduction or oxidation will convert one into another. This consideration has led Biddle (1913) to state that, "there seems to be thus an intimate connection between the properties on which the classification of plants is based and those which should naturally determine the classification of alkaloids. The interpretation of such relations will be much simpler, however, when the molecular structure of a much larger number of the plant bases is definitely known."

The alkaloids occurring in any one genus are generally quite closely related: thus the various aconitines have been separated only from members of the genus *Aconitum*, which is noteworthy, in giving a new chemical species of aconitine for each new botanical species analyzed, though all the aconitines are apparently closely related. An idea of the value of alkaloids (chemical characters) as complements of morphological characters in taxonomy may be gained by the study of two papers dealing with the revision of the genus *Cinchona*, viz., that of Rusby (1932) versus Standley (1931).

The same alkaloid is seldom found in different plant families, but on the contrary an alkaloid is often characteristic of one family, e.g., protopine occurs in many plants of the Papaveraceae and is not found in other families.

Where different alkaloids are met with in the same family each is generally confined to a single genus, and a better classification of these alkaloids is therefore obtained by dividing the family according to genera. In large families the alkaloids of the different genera are usually in close agreement when grouped according to tribes. For instance:

Papaveraceae

Subfamily II. Paperoideae:

Tribe 1, Eschscholtzieae: (ionidine, $C_{11}H_{25}O_4N_4$) *Eschscholtzia*

Tribe 2, Chelidoneae: (methoxychelidonine, $C_{21}H_{21}O_6N$) *Chelidonium*

Tribe 3, Papaveraceae: (glaucine, $C_{21}H_{25}O_4N$) *Glaucium*, (codamine, $C_{21}H_{25}O_4N$) (tritopine, $C_{42}H_{54}O_7N_2$) (lanthopine, $C_{23}H_{25}O_4N$) (narcotine, $C_{22}H_{23}O_7N$) (laudanosine, $C_{21}H_{27}O_4N$) (cryptopine, $C_{21}H_{23}O_5N$) (laudanine, $C_{20}H_{25}O_4N$) (papaverine, $C_{20}H_{21}O_4N$) (protopine, $C_{20}H_{19}O_5N$) (pseudomorphine, $C_{17}H_{18}O_3N$) (morphine, $C_{17}H_{19}O_3N$) (codeine, $C_{18}H_{21}O_3N$) (isothebaine, $C_{19}H_{21}O_3N$) (thebaine, $C_{19}H_{21}O_3N$), *Papaver*

Subfamily III. Fumarioideae:

(dicentrine, $C_{20}H_{21}O_4N$) *Dicentra*, (corycavine, $C_{23}H_{23}O_6N$) (corydaline, $C_{22}H_{27}O_7N$) (dehydrocorydaline, $C_{22}H_{25}O_5N$) (corycavidine, $C_{22}H_{25}O_5N$) (corybulbine, $C_{21}H_{25}O_4N$) (isocorybulbine, $C_{21}H_{25}O_4N$) (corycavanine, $C_{21}H_{21}O_5N$) (isocordine, $C_{20}H_{23}O_4N$) (corydine, $C_{20}H_{23}O_4N$) (corytuberine, $C_{19}H_{21}O_4N$) (bulbocapinine, $C_{19}H_{19}O_4N$) *Corydalis*

Solanaceae

Tribe 2, Solaneae: (atropine, $C_{17}H_{23}O_3N$) (tropine, $C_8H_{15}ON$) (belladonine, $C_{17}H_{21}O_2N$) *Atropa*, (hyoscyamine, $C_{17}H_{23}O_3N$) (tropine, $C_8H_{15}ON$) (nor-hyoscyamine, $C_{16}H_{21}O_2N$) (hyoscine, $C_{17}H_{21}O_4N$) *Hyoscyamus*, (solanidine, $(C_{15}H_{31}ON)_2$) (solanine, $C_{54}H_{92}O_{18}N_2$) *Solanum*

Tribe 4, Cestreae: (nicotine, $C_{10}H_{14}N_2$) (nicoteine, $C_{10}H_{12}N_2$) (nicotelline, $C_{10}H_8N_2$) *Nicotiana*

Leguminosae

Subfamily I. Mimosoideae:

Tribe 6, Parkieae: (paucine, $C_{27}H_{39}O_5N_5$) *Pentaclethra*

Subfamily III. Papilionatae:

Tribe 1, Sophoreae: (ormosine, $C_{20}H_{33}N_3$) *Ormosia*, (matrine, $C_{15}H_{24}ON_2$) *Sophora*

Tribe 2, Podalyrieae: (lupanine, $C_{15}H_{24}ON_2$) (lupinine, $C_{21}H_{40}O_2N_2$) (lupinidine, $C_{15}H_{26}N_2$) (spathulatine, $C_{33}H_{64}O_5N_4$) *Lupinus*, (spar-

teine, $C_{15}H_{26}N_2$) *Spartium*, (retamine, $C_{15}H_{26}ON_2$) *Retama*, (sarothamnine, $C_{15}H_{24}N_2$) (genistaine, $C_{16}H_{28}N_2$) *Sarothamnus*

Tribe 5, Loteae: (galegine, $C_6H_{13}N_3$) *Galega*

Tribe 7, Hedysareae: (arachine, $C_5H_{14}ON_2$) *Arachis*

Tribe 10, Phaseoleae: (hyaphorine, $C_{14}H_{18}O_2N_2$) *Erythrina*, (physovenine, $C_{15}H_{12}O_2N_8$) (eseramine, $C_{16}H_{25}O_2N_4$) (eserine, $C_{15}H_{21}O_2N_3$) (isophysostigmine, $C_{15}H_{21}O_2N_3$) (geneserine, $C_{15}H_{21}O_2N_3$) (eseridine, $C_{15}H_{23}O_3N_3$) *Physostigma*

Rubiaceae

Subfamily I. Cinchonoideae:

Tribe 3, Rondeletieae: (aribine, $C_{23}H_{20}N_4$) *Arariba*

Tribe 5, Cinchoneae: (cinchonidine, $C_{19}H_{22}ON_2$) (cinchonine, $C_{19}H_{22}ON_2$) (cinchotine, $C_{19}H_{24}ON_2$) (quinine, $C_{20}H_{24}O_2N_2$) (quinidine, $C_{20}H_{24}O_2N_2$) *Cinchona*, (cinchonine, $C_{19}H_{22}ON_2$) (quinine, $C_{20}H_{24}O_2N_2$) (cinchotine, $C_{19}H_{24}ON_2$) (concusconine, $C_{22}H_{26}O_4N_2$) (chairamine, $C_{22}H_{26}O_4N_2$) (conchinamine, $C_{19}H_{24}O_2N_2$) (chinamine, $C_{19}H_{24}O_2N_2$) (cupreine, $C_{19}H_{22}O_2N_2$) (diconchinine, $C_{40}H_{46}O_3N_4$) (homochinine, $C_{39}H_{46}O_4N_4$) (conchairamidine, $C_{22}H_{26}O_4N_2$) *Remijia*, (hymenodictine, $C_{23}H_{40}N_2$) *Hymenodictyon*, (corynantheine, $C_{22}H_{28}O_4N_2$) (hydroyohimbine, $C_{21}H_{28}O_3N_2$) (mesoyohimbine, $C_{21}H_{26}O_3N_2$) (isoyohimbine, $C_{21}H_{26}O_3N_2$) *Corynanthe*

Tribe 6, Naucleeae: (mitraversine, $C_{22}H_{26}O_4N_2$) (mitragyrine, $C_{23}H_{31}O_5N$) *Mitragna*, (rhynchophylline, $C_{22}H_{28}O_4N_2$) *Ourouparia*

Tribe 15, Psychotrieae: (cephaeline, $C_{28}H_{38}O_4N_2$) (psychotrine, $C_{28}H_{36}O_4N_2$) (emetine, $C_{30}H_{40}O_4N_2$) *Cephaelia*

A small number of alkaloids occur in various plants which possess no close botanical relationships to each other. Some of these seem to have no particular physiological activity. The purine alkaloids caffeine and theobromine supply an instance of closely related alkaloids occurring in plants belonging to widely different (tropical) families. Some alkaloids are found in the same orders, e.g., bebeerine and laurotetanine are both found in the Ranales. Other alkaloids each of which is found in two or more families are: (tropical) brucine (molecular weight 394), bebeerine (297), laurotetanine (327), and yohimbine (368); (temperate) (canadine (339), chelidonine (353), chelerythrine (347), homochelidonine (369), and narceine (445), and (widely distributed) allantoine (158), bebeerine (353), choline (121), cytisine (190), hordeine (165), sanquinarine (333), stachydrine (143), and trigonelline (137).

It has been suggested by Pictet and Biddle (1913) that some of these, namely, the members of the purine, choline, and asparagine groups, differ

from the more specific alkaloids in appearing not to be *assimilation products* of the plant organism, but *decomposition products* of more complicated derivatives.

In support of the Pictet and Biddle suggestion, it is evident that in the animal metabolism purine bodies, such as uric acid, which appear in the urine are decomposition products from compounds of larger molecular weights. Choline, widely distributed in the animal and vegetable kingdoms, is a decomposition product of lecithine, is contained in hops, and also in the alkaloid sinapine, which occurs in mustard seeds; it is produced in corpses, as the result of putrefactive changes.

It is interesting to note that the average molecular weights, of the alkaloids which are found in more than one plant family, are lower than the average molecular weights of the other alkaloids which are confined to individual families in the same climate of habitat. A similar statement applies to the alkaloids of maximum molecular weight.

These low molecular weights of alkaloids of wide botanical distribution certainly indicate that the more simple alkaloids are more widely distributed than the more complex. These simpler alkaloids may perhaps be either the decomposition products of more complex substances or the nuclei (building stones) of more complex compounds.

SUMMARY

Alkaloids are found in fifty-seven families of gymnosperms and angiosperms; of these 44% are mostly tropical and 14% are temperate.

The ratio of tropical alkaloidal families to the total tropical families (16.34%) is practically the same as the ratio of temperate alkaloidal families to the total temperate families (16.0%).

The maximum and average molecular weights increase markedly from tropical to temperate, while the minimum registers a slight decrease.

The average and minimum number of carbon atoms is the same for both tropical and temperate alkaloids while the maximum decrease from tropical to temperate.

The minimum and average numbers of hydrogen atoms increase from tropical to temperate while the maximum numbers indicate a decrease.

The maximum, minimum, and average numbers of oxygen atoms increase from tropical to temperate.

Both the average and minimum values for nitrogen are the same in both tropic and temperate families but the maximum decreases from tropical to temperate.

Alkaloids are found in 40% of the gymnosperm families, 11% of the

TABLE 1

Variations in the composition of alkaloids in relation to climate of habitat

HABITAT	MOLECULAR WEIGHT			CARBON			HYDROGEN			OXYGEN			NITROGEN		
	MAX.	MIN.	AVER.	MAX.	MIN.	AVER.	MAX.	MIN.	AVER.	MAX.	MIN.	AVER.	MAX.	MIN.	AVER.
Tropical	634	121	333	36	8	17	55	11	22	6	0	2	4	1	1
Tropical-subtropical	572	135	243	18	5	10	21	5	14	5	1	2	4	1	2
Subtropical	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Subtropical-temperate	669	285	376	37	18	25	51	25	40	10	2	5	2	1	1
Temperate	698	125	379	29	8	17	39	17	24	11	0	5	2	1	1
Widely distributed	1057	118	320	32	7	17	41	13	21	13	0	4	3	1	2

monocotyledons, and 18% of the dicotyledons. The molecular weights are larger in the angiosperms than in the gymnosperms.

Alkaloids in the same plant generally bear the closest chemical relation to one another.

Alkaloids found in any one genus are usually somewhat closely related.

The same alkaloid is rarely met with in different plant families.

Where different alkaloids are met with in the same family they are generally each confined to a single genus.

In large families the alkaloids of the different genera are usually in close agreement when grouped according to tribes.

A small number of these compounds are found in more than one family.

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Additional notes on tautonyms

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In April, 1932, I published an article entitled "A discussion of tautonyms"[1] in which 228 of these bizarre binomials were listed, together with what I considered to be the oldest valid non-tautonymous name within the given genus for the plant in question in each case. In March, 1934, in an article entitled "A supplementary list of tautonyms and miscellaneous nomenclatural notes"[2] thirteen more such tautonyms were listed.

Since these two papers went to press, a number of inaccuracies in the first of them have been called to my attention. Among these are eight cases where the given tautonymous combination was validly published previous to the citation given by myself in my original list. Although in almost every case one will find, if one looks up the reference cited by myself, that the tautonymous combination is actually proposed there as a new one, yet these proposals appear upon further investigation to have been made in ignorance of the fact that the proposed binomials had already been published previous to that date. The following, then, are the correct citations for these eight tautonyms:

CEDRUS CEDRUS (L.) Huth, Helios **11:** 133. 1893.

CYDONIA CYDONIA (L.) Pers. Syn. Pl. **2:** 40. 1807.

DAMASONIUM DAMASONIUM (L.) Aschers. & Graebn. Syn. Mitteleur. Fl. **1:** 389. 1898.

LYCOPERSICON LYCOPERSICON (L.) Karst. ex Lyons, Pl. Names 232. 1900.

MALUS MALUS (L.) Britton in Britton & Br. Ill. Fl., ed. 1, **2:** 236. 1897.

VACCARIA VACCARIA (L.) Huth, Helios **11:** 136. 1893.

VANILLA VANILLA (L.) Huth, Helios **11:** 136. 1893.

VITIS-IDAEA VITIS-IDAEA (L.) Britton, Man. 708. 1901.

In addition to the binomials mentioned above, the following have also been proposed as new more than once, and the citations given below will often be found quoted as the correct ones for the binomials in question. In each of the following cases, however, the combination is antedated by the reference cited by me in my original list. The references below are given here merely as a matter of record.

Abies Abies (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles **7:** 689. 1925.

Abutilon Abutilon (L.) Rusby, Mem. Torrey Club **5:** 222. 1894.

Adhatoda Adhatoda (L.) Lyons, Pl. Names 15. 1900.

Alliaria Alliaria (L.) Britton, Mem. Torrey Club **5:** 167. 1894.

Ananas Ananas (L.) Lyons, Pl. Names 32. 1900.

[1] Bull. Torrey Club **59:** 139–156.

[2] Torreya **34:** 5–10.

Arisarum Arisarum (L.) Dörfler, Herb. Norm. No. 3270. 1897.
Castanea Castanea (L.) Sudworth, Bull. Torrey Club **19:** 152. 1892.
Castanea Castanea (L.) Lyons, Pl. Names 85. 1900.
Cedrus Cedrus (L.) Lyons, Pl. Names 88. 1900.
Cetarach Cetarach (L.) Lyons, Pl. Names 92. 1900.
Colocasia Colocasia (L.) Lyons, Pl. Names 111. 1900.
Corallorhiza Corallorhiza (L.) MacM., Bull. Torrey Club **19:** 15. 1892.
Cotinus Cotinus (L.) Karst. ex Lyons, Pl. Names 119. 1900.
Cubeba Cubeba (L. f.) Lyons, Pl. Names 124. 1900.
Cydonia Cydonia (L.) Lyons, Pl. Names 127. 1900.
Dracunculus Dracunculus (L.) Druce, Brit. Pl. List, ed. 2, 115. 1928.
Eragrostis Eragrostis (L.) MacM. Metasp. Minn. 75. 1892.
Eragrostis Eragrostis (L.) Karst. Deutsch. Fl. 389. 1881.
Filipendula Filipendula (L.) Aschers. & Graebn. Syn. Mitteleur. Fl. **6**[1]**:** 439. 1902.
Lagenaria Lagenaria (L.) Lyons, Pl. Names 213. 1900.
Lens Lens (L.) Lyons, Pl. Names 219. 1900.
Leontopodium Leontopodium (L.) Lyons, Pl. Names 219. 1900.
Levisticum Levisticum (L.) Lyons, Pl. Names 223. 1900.
Limonium Limonium (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles **7:** 583 & 687. 1925.
Malvaviscus Malvaviscus (L.) Millsp., Field Columb. Mus. Pub. Bot. **2:** 73. 1900.
Manihot Manihot (L.) Lyons, Pl. Names 239. 1900.
Moringa Moringa (L.) Small, Fl. SE. U.S. 491. 1903.
Nelumbo Nelumbo (L.) MacM. Metasp. Minn. 226. 1892.
Omphalodes Omphalodes (L.) Druce, Rep. Bot. Exch. Cl. Brit. Isles **7:** 688. 1925.
Opopanax Opopanax (L.) Lyons, Pl. Names 266. 1900.
Opuntia Opuntia (L.) Coult., Contr. U.S. Nat. Herb. **3:** 432. 1896.
Petroselinum Petroselinum (L.) Lyons, Pl. Names 282. 1900.
Phragmites Phragmites (L.) MacM. Metasp. Minn. 73. 1892.
Pimenta Pimenta (L.) Lyons, Pl. Names 290. 1900.
Pyracantha Pyracantha (L.) Aschers. & Graebn. Syn. Mitteleur. Fl. **6**[2]**:** 11. 1906.
Taraxacum Taraxacum (L.) MacM., Bull. Torrey Club **19:** 15. 1892.
Thevetia Thevetia (L.) Lyons, Pl. Names 370. 1900.
Ugni Ugni (Mol.) Macloskie, Rep. Princeton Univ. Exped. Patag. **8:** 602. 1905.
Viscaria Viscaria (L.) Degen., Magyar Bot. Lap. **4:** 122. 1905.
Zingiber Zingiber (L.) Rusby ex Lyons, Pl. Names 402. 1900.

It is also worth noting that a rather serious orthographic error occurs on page 147 of my first list, where the name "LEPTOSTACHYS LEPTOSTACHYS" is recorded and accredited to MacMillan. *Leptostachys* is a generic name proposed by G. F. W. Meyer in the *Gramineae* and by Ehrhart in the *Cyperaceae*. In neither case has the above-mentioned tautonymous combination been proposed. The binomial which MacMillan proposed and to which I referred in my list was *Leptostachya Leptostachya*, a synonym of *Phryma Leptostachya* L. [*Leptostachya carolinensis* Kuntze] in the *Phrymaceae*.

As a matter of record, it should also be noted that the orthographic variant "*Ecastaphyllum Ecastaphyllum*" appears in the Index Kewensis, although in the reference there cited one finds that the binomial as originally proposed by Huth was written *Ecastophyllum Ecastophyllum*.

The following additional tautonyms, never before listed by myself, have come to light since the publication of my second article on this subject:

CALCITRAPA CALCITRAPA Hill, Hort. Kew. 62. 1768.
=*Calcitrapa stellaris* Hill, Herb. Brit. **1:** 76. 1769.

CROCODYLIUM CROCODYLIUM (L.) Hill, Hort. Kew. 63. 1768.
=*Crocodilium syriacum* Cass., Dict. Sci. Nat. **12:** 19. 1818.

ERIOPHA ERIOPHA Hill, Hort. Kew. 69. 1768.[3]
=*Centaurea eriophora* L. Sp. Pl. 916. 1753.

RHAPONTICA RHAPONTICA (L.) Hill, Hort. Kew. 69. 1768.
=*Rhaponticum scariosum* Lam. Fl. Fr. **2:** 38. 1778.

On page 147 of his "Hortus Kewensis" Hill lists under the generic name *Mandragora* one species, as follows: "1. *Mandragora. Atropa Mandragora.*" On page 148 he cites under the generic name *Battata* one species in the same manner: "1. *Battata. Solanum Tuberosum.*" The Index Kewensis considers the latter as valid publication of "*Battata tuberosa* Hill." If this is so, then the former is certainly valid publication of "*Mandragora Mandragora* Hill," a combination not listed in the Index Kewensis. The inconsistency of the Index Kewensis in its policy toward this work of Hill is well illustrated by the following additional example. On page 148, under the genus *Lycopersicum*, Hill again cites only one species, as follows: "1. *Lycopersicum. Solanum Lycopersicum.*" This the Index Kewensis lists as "*Lycopersicum Solanum-Lycopersicum* Hill"!

In several instances the non-tautonymous names which I gave as the correct ones in that particular genus in my original list have been found to

[3] Hill implies that this is a new combination for "*Centaurea Eriopha*," but no such name was ever published as far as I have been able to ascertain. The species referred to was undoubtedly Linnaeus' *Centaurea eriophora*. The genus *Eriopha* is not maintained by anyone today and no other binomials have even been published in it.

be antedated by other binomials. For the sake of accuracy I am listing these tautonyms again below, together with the non-tautonymous binomials which further investigations have revealed to be the correct ones in each instance:

ANANAS ANANAS (L.) Voss, Vilmorin's Blumeng., ed. 3, **1:** 964. 1895.
= *Ananas comosus* (L.) Merr. Interpret. Rumph. Herb. Amb. 133. 1917.

HELENIUM HELENIUM (Nutt.) Small, Fl. SE. U.S. 1292 & 1341. 1903.
= *Helenium decurrens* (Macbride) Moldenke.[4]

OXYCOCCUS OXYCOCCUS (L.) MacM., Bull. Torrey Club **19:** 15. 1892.
= *Oxycoccus quadripetalus* Gilib. Fl. Lithuan. **1:** 5. 1781.

PERSEA PERSEA (L.) Cockerell, Bull. Torrey Club **19:** 95. 1892.
= *Persea americana* Mill. Gard. Dict., ed. 8. 1768.

POROPHYLLUM POROPHYLLUM (L.) Kuntze, Rev. Gen. Pl. **3**[2]: 168. 1898.
= *Porophyllum ruderale* (Jacq.) Cass., Dict. Sci. Nat. **43:** 56. 1826.

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[4] **Helenium decurrens** (Macbride) Moldenke, comb. nov. *Leptopoda decurrens* Macbride ex Ell. Bot. S. C. & Ga. **2:** 446. 1824. This is the plant originally called *Leptopoda Helenium* Nutt. [Gen. **2:** 174. 1818] and then *Leptopoda helenioides* Cass. [Dict. Hist. Nat. **26:** 80. 1823]. The combination *Helenium Helenium* (Nutt.) Small cannot be used because it is a tautonym, and the use of *Helenium helenioides* is precluded by the *Helenium helenioides* of Clements & Clements [Rocky Mt. Fl. 279. 1914], an entirely different species of the Rocky Mountains.

INDEX TO AMERICAN BOTANICAL LITERATURE
1931–1935

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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